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Effects of catchment clearing and sedimentation on macroinvertebrate communities of cobble habitat in freshwater streams of southwestern Australia

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Abstract

The removal of riparian vegetation from along first order streams of the northern jarrah forest reduced ecological health, as assessed by an examination of cobble communities. Macroinvertebrate diversity was significantly lower in cleared compared to uncleared reaches. There was also an associated decrease in the biomass and a change in the composition of epilithon communities, from those dominated by the angiosperm *Potamogeton ?crispus* to thin slimes dominated by diatoms. Extensive growths of filamentous algae were not observed on cobbles in cleared reaches. Species of Odonata, Ephemeroptera, Trichoptera and Chironomidae were the most notable absences from cobbles in cleared reaches. Grazer abundance also was reduced. Few species in cobble habitats appeared to benefit from catchment clearing although there was a significant increase in the abundance of the undescribed chironomid Orthocladiinae V61, which may be a useful indicator species. We also tested the effect of short term elevations in suspended sediment through experimental addition of sediment in an attempt to separate the effects of sediment from others related to catchment clearing. There was no significant difference in macroinvertebrate diversity between control and sediment-added cobbles, and both had higher diversity than cobbles in cleared reaches. We concluded that the changes in the epilithic cover in cleared reaches caused indirectly the changes in the macroinvertebrate community, either through a change in the composition of food sources or loss of refugia. Sedimentation in cobble environments might have greater impact in the longer term than noted in this study, and also might have impact on other stream meso-habitats.

Keywords: macroinvertebrate communities, freshwater streams, cobble habitats, catchment clearing, southwestern Australia

Introduction

The importance of riparian zones is well recognised in stream ecology. They provide a critical link between terrestrial and aquatic ecosystems (Lynch & Catterall 1999), and largely control the functioning of the latter. Riparian cover has a strong influence on stream productivity (Bunn *et al.* 1999a), providing shade that maintains lower water temperature (Bunn *et al.* 1999b) and reduces light penetration, thereby controlling algal growth (Mosisch *et al.* 1999). Riparian zones also provide an important allochthonous food source for some aquatic animals (Lake 1995) and increase habitat heterogeneity (Likens & Bormann 1974; Lake & Marchant 1990; Gregory *et al.* 1991). Vegetated stream banks are more stable than those without vegetation (Abernathy & Rutherford 1999). They moderate the flow of sediment and nutrients into the water column (Gregory *et al.* 1991; Waters 1995), and filter nutrients from surface and groundwater flows (Prosser *et al.* 1999). In eastern Australia, even narrow riparian buffers are effective at trapping overland flows of sediment (Prosser *et al.* 1999).

Loss of or disturbance to riparian vegetation therefore has many effects, one of the more obvious being the periodic increase in turbidity and bed-load sediment transport, particularly during rainfall events (Brown 1972; Karr & Schlosser 1978; Lemly 1982; Campbell & Doeg 1989; Hogg & Norris 1991; Quinn *et al.* 1992). Increased sediment loads are known to have detrimental effects on both aquatic macroinvertebrates (e.g. McLelland & Brüsven 1980; Lenat *et al.* 1981; Lemly 1982) and aquatic plants and algae (Lewis 1973a,b; Nutall 1972; Graham 1990). In many instances, stream macroinvertebrates respond to increased sediment levels by drifting (e.g. Gray & Ward 1982; Doeg & Milledge 1991).

Removal of streamside vegetation can have different effects among mesohabitat scale communities (Lenat *et al.* 1981; Lemly 1982). The present study focussed on the cobble meso-habitat (*sensu* Cummins 1962), which has been identified as a discrete 'natural unit' due to a 'well defined, abrupt boundary' (Davies 1994). Cobbles are characterised by a comparatively high projection and occur in regions of relatively high shear velocity in the stream channel (Davies 1994). A unique feature of cobbles is the provision of a stable substrate which enables growth of epilithic algae and aquatic plants. Cobbles also provide a stable platform from which sessile animals, such as filter feeders, may extract suspended food particles from the water column (Wallace & Merritt 1980).

In the northern jarrah forest, macroinvertebrate and epilithic communities of cobbles are distinct from those of other stream habitats, being dominated by animals in

scraper and filterer feeding guilds in contrast to the dominance of collectors in riffles, and collectors and shredders in organic depositional habitats (Davies 1994). Cobbles are also characterised by a greater proportion of autochthonous (instream-derived) vegetative material compared with riffle and organic depositional habitats. The production to respiration ratio of cobble habitat is typically greater than one, indicative of autotrophy (*i.e.*, having a carbon source predominantly derived from instream photosynthetic processes; Davies 1994). In upland streams of the northern jarrah forest, the low nutrient status of soils and shading by the riparian canopy minimise the standing crop of epilithon compared with streams in eastern Australia (Bunn and Davies 1990). These characteristics make cobbles a useful unit for assessing the effects of removal of streamside vegetation on both macroinvertebrates and epilithic vegetation.

The construction of the North Dandalup Dam (south of Perth, Western Australia) provided an opportunity to investigate the effects of riparian vegetation removal on aquatic macroinvertebrate communities in northern jarrah forest streams. Dam construction involved the total clearing of 430 ha of riparian and upslope vegetation within the reservoir basin. It was predicted that elevated sedimentation associated with clearing would be detrimental to both the fauna and epilithon of cobbles. We compared the diversity of cobble macroinvertebrates and the composition of epilithon between cleared and uncleared reaches. It was also predicted that elevated sediment levels in the water column would have the greatest effect on the cobble habitat, since they are exposed above the streambed. Thus, we examined the short term effect of suspended sediment addition on the aquatic macroinvertebrate communities of cobble substrates in an attempt to distinguish this from other effects resulting from the removal of riparian vegetation.

Methods

Study area

The study area, situated *c.* 100 km south of Perth, consisted of three first order streams (Foster and Wilson Brooks and the North Dandalup River; Fig 1) in the North Dandalup catchment, a system of about 40 km in length. The headwater streams arise in swamps on the Darling Range (300 m above sea level), the south-western edge of the Great Plateau of Western Australia (Jutson 1950). The streams flow over lateritic soils and granite bedrock before descending through an incised river valley to the Swan Coastal Plain. The headwaters are located in the northern jarrah forest, a dry sclerophyll forest dominated by jarrah *Eucalyptus marginata* Sm. and to a lesser extent marri *Corymbia calophylla* (Lindl.) K.D. Hill & L.A.S. Johnson. The riparian understorey is composed of dense sclerophyllous shrubs, including *Agonis linearifolia* (DC.) Sweet, *Lepidosperma tetraquetrum* Nees and *Hypocalymma angustifolium* (Endl.) Schauer. The upper catchment has been selectively logged since European settlement and was the site of a small gold strike in the late 1800s. The area has a Mediterranean climate with wet, mild winters, hot, dry summers, and an annual rainfall of approximately 1100 mm. The

general geology and flora of the area has been summarised by Bunn (1986) and Storey *et al.* (1990).

The North Dandalup system has been regulated from 1971 by a small pipehead dam (capacity 20 000 m³). However, to serve the growing demand from the Perth metropolitan area, the pipehead dam was replaced in October 1994 by the North Dandalup Dam, a 62 m high rock-fill dam wall, forming a major water supply reservoir (catchment area 153 km², 510 ha surface area at full storage and a capacity of 75 GL), supplying 10% of the annual water consumption of Perth.

Sampling

The experimental design comprised three treatments: undisturbed upstream controls in uncleared reaches (CON), sediment addition in uncleared reaches (SED), and cleared or 'impact' reaches (IMP). Each treatment was replicated at three sites on each of the three streams. Each replicate consisted of three cobbles sampled at random from the stream bed, giving a total of nine cobbles per treatment per stream and a total of 81 cobbles sampled. Storey *et al.* (1990) have shown that macroinvertebrate communities of northern jarrah forest streams are generally homogeneous within the same stream order, and therefore it was anticipated that the three streams would be comparable replicates. All impact sites necessarily were located downstream of uncleared areas but within the same stream order. Sediment and control treatments were interspersed within the uncleared reaches. The sediment addition experiment was performed once only for each cobble between the 29th July–3rd of August and the 10th–11th of August, 1995. Other cobbles were sampled whilst moving upstream at this time, so that no unsampled cobbles were left downstream.

The short term elevation in turbidity was mimicked by the slow addition of fine (<2 mm) sediments to channel reaches containing cobbles. Approximately 60 kg of lateritic soil was washed into the water column over a two-hour period at distance of *c.* 1 m above the cobbles to be sampled. Total suspended sediment level was measured from water samples (dry weight per litre) collected downstream of the point of sediment addition to assess the effectiveness of the treatment. Cobbles were sampled two hours after the commencement of the sediment addition by removal of the cobble, using a D-frame pond net (250 mm mesh aperture) placed immediately downstream.

Within the cleared reaches, there were numerous cobbles that had only recently entered the stream through bank erosion/slumping or through the influence of heavy machinery. These lacked an obvious layer of epilithon, were not embedded in the stream and therefore were not sampled; only cobbles of lateritic composition with an established epilithic layer were sampled. Attached fauna were removed into a basin by scrubbing the cobble with a soft brush, and epilithon was removed with a harder brush and immediately preserved in 5% formalin. Macroinvertebrate specimens were identified to lowest possible taxonomic level (species, where possible), and vouchers lodged with the School of Animal Biology, The University of Western Australia. Taxa were then allocated to their appropriate functional feeding groups (ie. filterer and grazer; *sensu* Cummins
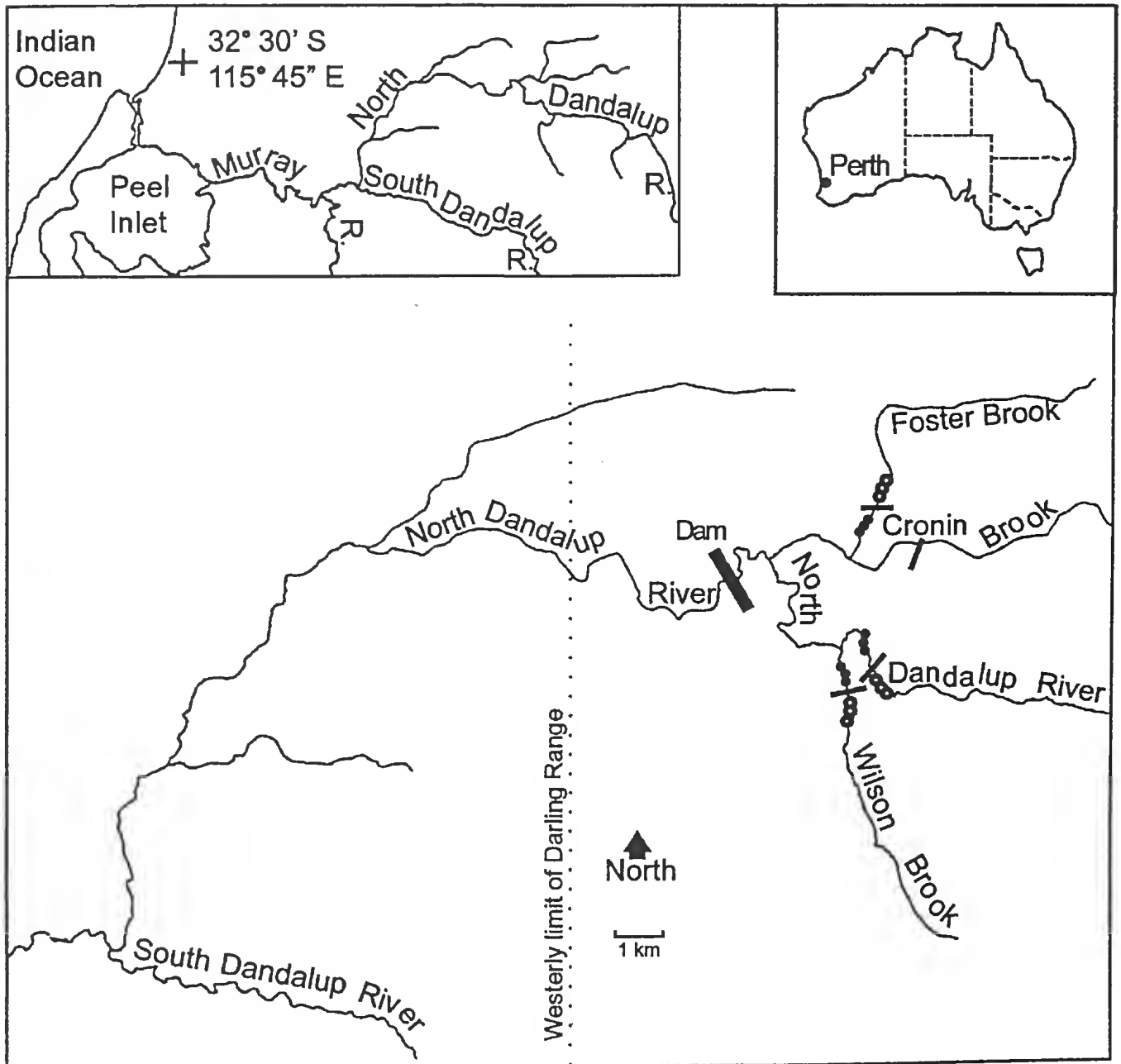
Figure 1. Location of the North Dandalup catchment and first order streams sampled in Western Australia. Bars indicate extent of catchment clearance in each stream, closed circles indicate sites where impact cobbles were sampled and open circles where control and sediment treatment cobbles were sampled.

1973, Merritt & Cummins 1978, Bunn 1985, 1986). To standardise the abundance of fauna between different-sized cobbles, the surface area of each cobble was determined in the field by wrapping it in aluminium foil and relating the weight of the foil to surface area by regression. Only the proportion of the rock surface exposed to the water was measured.

Physico-chemical variables were measured at each cobble before sampling. Conductivity (EC) dissolved oxygen (DO) and pH were measured with WTW conductivity, dissolved oxygen and pH meters respectively, and stream velocity at 5 cm above the substrate with a Marsh McBirney portable water flow meter (model 201). Total Phosphorus (by potassium persulphate digestion with subsequent orthophosphate

assay using the molybdenum blue method; Wetzel & Likens 1979) and total Kjeldahl nitrogen (by digestion with ammonia subsequently assayed using an ammonia-sensitive electrode; Bremner & Mulvaney 1982) were measured from each stream. Two samples from the water surface were taken at the downstream end of each treatment area.

Analysis

For statistical analysis, the type of epilithic cover was recorded as either 'algae', 'diatom matrix', 'Potamogeton', 'Nostoc' or 'no epilithon'. Chi-square analysis was used to detect departures in observed from expected frequency of occurrence for each epilithon type in each treatment. Two-way ANOVA was used to test for treatment and

sub-catchment (stream) differences in epilithon biomass (per square metre), as well as macroinvertebrate community parameters (abundance, richness, Shannon-Weiner diversity (Shannon & Weiner 1949), chironomid richness and abundance, and the abundance of filterers and grazers), with 'treatment' and 'stream' as fixed factors. Where there were significant main effects, Tukey's HSD multiple range tests were applied *a posteriori* to detect treatment and sub-catchment differences in community parameters. All data were $log_{10}(x+1)$ transformed prior to analysis to achieve equality of variances (Cochran's C test for homoscedasticity). All the above analyses were undertaken in the SAS statistical package (SAS, 1994). Ordination of samples based on macroinvertebrate community composition was undertaken using hybrid non-metric Multi Dimensional Scaling (MDS) in the PATN analysis program (Belbin 1995), with pairwise similarities amongst samples calculated using the Bray-Curtis similarity index. The separation of treatments in ordination space was tested using Analysis of Similarity (ANOSIM) (Belbin, 1995). Gradients in environmental variables (DO, EC, pH and stream velocity) and community descriptors were fitted through ordination plots using the Principle Axis Correlation (PCC) option in PATN, with Monte Carlo randomisations (n=100) of the data performed to test the significance of the gradients. A separate ordination was performed for each subcatchment (stream) due to the observed differences between streams. Ordinations were performed to minimise dimensions and stress, and plotted to display those dimensions that illustrated the greatest separation of treatments.

Results

Physico-chemical

The turbidity of the water column two metres downstream from the point of sediment addition increased significantly during sediment addition compared with control and cleared sites (two-way ANOVA: $F_{2,25}$ = 4.5, p = 0.03; means ± S.E.: SED 26.8 ± 4.0 mg L^{-1}; CON 12.0 ± 4.6 mg L^{-1}; IMP 11.0 ± 2.4 mg L^{-1}). Bedload transport was also observed to be much higher (as might be expected) but was not quantified. Total phosphorus and total Kjeldahl nitrogen were both < 10 mgL^{-1} for all treatments (K. Armstrong unpublished data).

Epilithon

Four dominant types of epilithic growth were recorded. Most cobbles in uncleared reaches supported growths of the aquatic angiosperm *Potamogeton ?crispus* (Potamogetonaceae). When present, this species dominated the cobble epilithon community. On cobbles where *Potamogeton ?crispus* was absent, chlorophytes were the dominant epilithic growth. In this study, chlorophytes were classified into two main types; 'Nostoc' which had a nodular growth form similar to that of *Nostoc* and 'algae' which included all remaining Chlorophyta. The majority of cobbles in cleared reaches lacked an epilithon layer although many were covered in a thin, slimy matrix of diatoms, bacteria and accumulated sediments. The sediment addition was a short term treatment, and therefore had no effect on epilithon.

There was a significant departure from expected frequency for the types 'Potamogeton', 'diatom matrix' and 'no epilithon' (Table 1). In each instance, the departure from expected occurred in the impact reach, with more than the expected number of cobbles dominated by 'diatoms' or with 'no epilithon', and fewer than expected cobbles being dominated by '*Potamogeton*' (Table 1). Associated with the change in epilithon type was a decrease in biomass in the impact treatment (Table 2).

Macroinvertebrate fauna

The total number of taxa and total abundance per m^2 recorded in controls (98 taxa and 26 556 individuals m^{-2}) was greater than in both sediment and impact treatments (87 taxa and 26 748 individuals m^{-2}, and 72 taxa and 12 498 individuals m^{-2} respectively). The proportion of taxa in common between control and impact treatments was 66 %, and between control and sediment addition treatments was 86 %. Notable absences from impact cobbles compared to controls included the mayfly *Bibulmena kadjina*, the trichopteran *Plectrotarsus minor*, the dragonfly *Argiolestes minimus*, the caddisfly *Ecnomina sentosa* type group and the chironomid *Riethia ?zeylandica*.

All community parameters showed a significant treatment effect, and the majority a significant stream effect, with no significant interactions (Table 2). In general, the impact treatment had the lowest taxonomic richness and total densities of any parameter (Figure 2). There were 20 taxa with significant subcatchment and/or treatment differences in abundance (Table 3). Of these, 10 species had a higher abundance in control than impact

Table 1

Analysis of the frequency of occurrence of dominant epilithon types on cobbles from Control, Impacted and Sedimented reaches, giving χ^2 statistic, significance level and Observed/Expected number of occurrences in each treatment. *: indicates the cell that has the greatest contribution to the total χ^2-statistic.

Epilithon Type	χ^2	P	Control	Impact	Sediment
Algae	0.75	ns	3 / 3	4 / 3	2 / 3
Diatom matrix	15.32	0.0005	0 / 2.3	7 / 2.3*	0 / 2.3
Nostoc	1.28	ns	6 / 4.3	3 / 4.3	4 / 4.3
Potamogeton	32.34	< 0.0001	18 / 13	1 / 13*	20 / 13
No epilithon	24.37	< 0.0001	0 / 4.3	12 / 4.3*	1 / 4.3

Table 2

Analysis of various community parameters by sub-catchment (F: Foster, W: Wilson and N: Nth Dandalup) and treatment (C: Control, I: Impact, S: Sedimented). Tukey's multiple comparison test was used to locate between-level differences for significant main effects. The order of levels within each parameter has been standardised according to that indicated for the first parameter, and a common line joins levels not significantly different. Significance of main effects and interaction terms are indicated by: ns: not significant, *: P < 0.05, **: P < 0.01 and ***: P < 0.001.

Parameter	Sub-catchment (df=2)	Treatment (df=2)	Interaction	Sub-catchment	Treatment
				W N F	C S I
Epilithon biomass (m^2)	7.0**	9.4***	0.7ns		
Abundance (m^2)	7.4**	10.7***	1.7ns		
Number of taxa	4.3*	26.2***	2.5ns		
Shannon-Weiner Diversity	0.9ns	16.7***	1.7ns		
Chironomid richness	14.5***	11.9***	1.3ns		
Chironomid abundance (m^2)	2.5ns	3.4*	1.1ns		
Grazer abundance (m^2)	18.9***	18.2***	2.5ns		
Filterer abundance (m^2)	3.8*	5.1**	0.03ns		

Table 3

Differences in the abundance of selected invertebrate species (F: Foster, W: Wilson and N: Nth Dandalup) and treatment (C: Control, I: Impact, S: Sedimented) on $\log_{10}(x+1)$ abundance of each taxon (ns: p>0.05, *: p<0.05, **: p<0.01, ***: p<0.0001). The order of levels within each parameter has been standardised according to that indicated for the first parameter, and levels of main effects not significantly different, as determined by Tukeys multiple range (a<0.05) are joined by a common line. Voucher specimens are lodged in the Aquatic Research Laboratory, School of Animal Biology, The University of Western Australia.

Taxon	Sub-catchment	Treatment	Interaction	Sub-catchment	Treatment
				W N F	C S I
A090102	ns	*	ns		
Austrosimulium sp. X	*	**	ns		
Ceratopogonidae sp. A	*	**	ns		
Ecnomus turgidus	ns	**	ns		
ND 307 Hydracarina ND ?	*	*	ns		
Neboisiphlebia sp. Ngunurra sp. combined	***	***	ns		
Ostracoda sp.	*	ns	ns		
Smicrophylax australica	**	ns	ns		
Tasmanocoenis tillyardi	***	ns	ns		
Botryocladus bibulmun	ns	**	ns		
Thienemanniella sp.V19	***	ns	ns		
Nilothauma sp.V21	**	ns	ns		
?Paralimnophyes sp.V31	***	***	ns		
Limnophyes pullulus V42	**	ns	ns		
Dicrotendipes sp.V47	**	ns	ns		
Riethia sp. nov. V5	ns	***	ns		
Tanytarsus spp.V6	***	**	ns		
Orthocladiinae V61	ns	*	ns		
Stempellina ?australiensis	ns	*	ns		
Orthocladiinae VND1	**	ns	ns		

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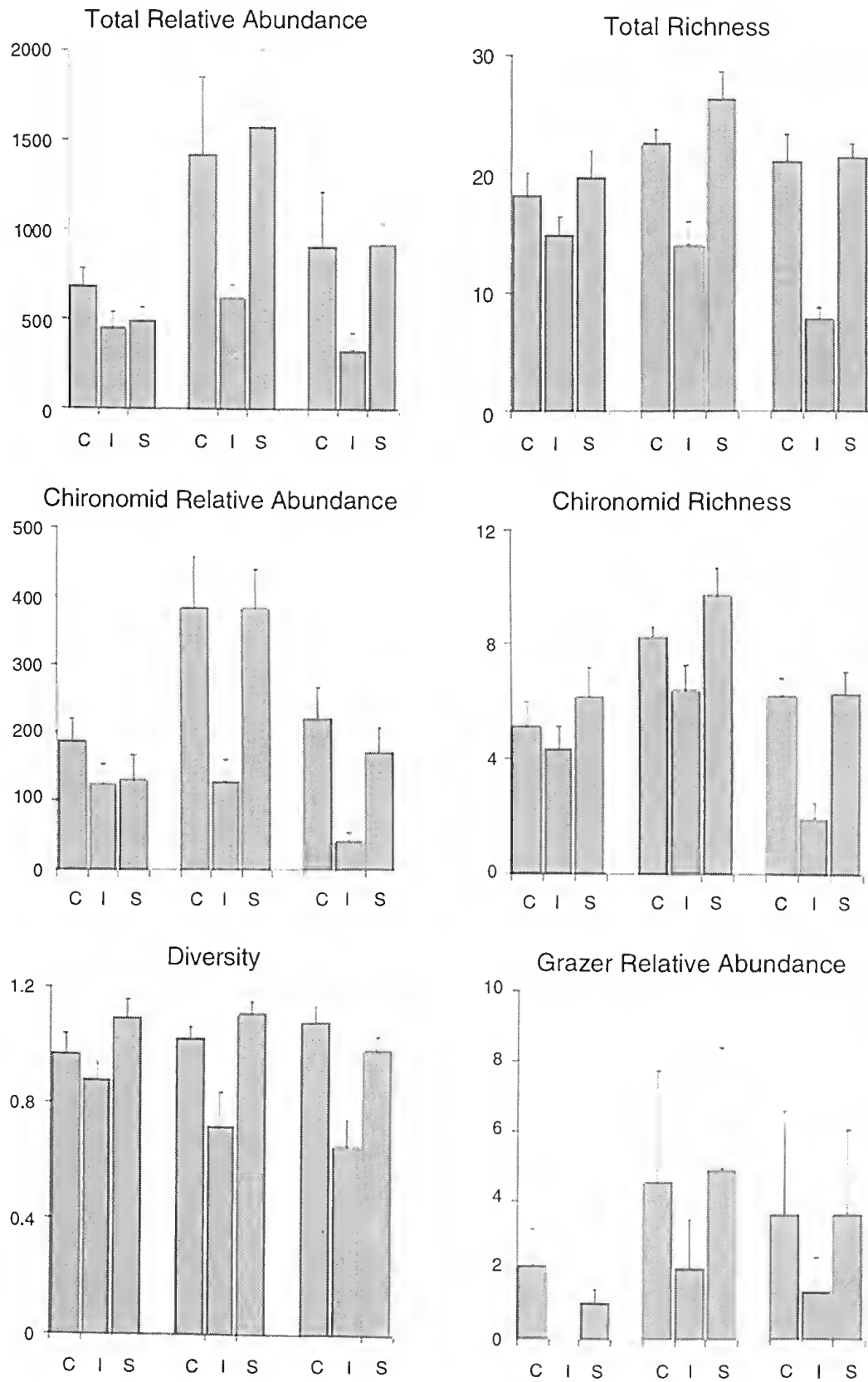
Figure 2. Comparison of some community descriptors between treatments. Within each plot, histograms are grouped by stream (Foster, North Dandalup and Wilson, respectively) and labelled according to treatment (control (C), impact (I) and sediment addition (S)). Values are means ± 1 S.E.
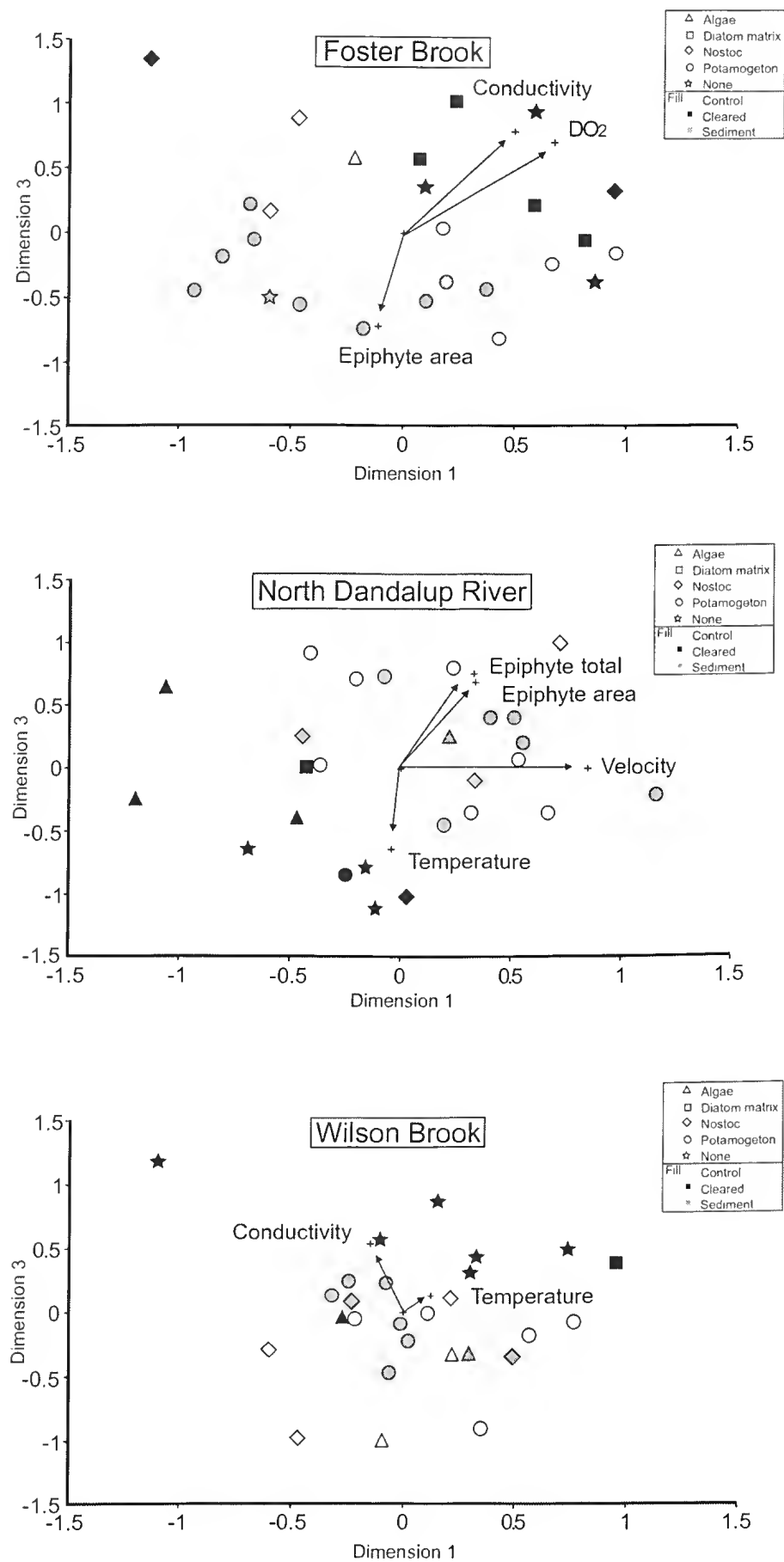
Figure 3. MDS ordination plots from PATN illustrating the similarity of each cobble sample. Physical variables appear as gradients. Stress values: Foster: 0.19; North Dandalup: 0.16; Wilson: 0.14.

treatment. The chironomid Orthocladiinae V61 showed a positive response to catchment clearing, increasing significantly in abundance in the impact reaches.

Ordination

Initial analyses (two-way ANOVAs and ordinations) showed significant differences between streams. Therefore, streams were treated in isolation for subsequent multivariate analysis. For each stream there was a clear separation of impact cobbles from both control and sediment addition cobbles, indicating differences in the composition of macroinvertebrate communities following clearing (Figure 3). ANOSIM testing between treatments was significant in the case of all three streams (Foster and North Dandalup: P<0.0001; Wilson: P<0.01). There was some separation of control and sediment addition cobbles in Foster Brook, however this pattern was not observed in the other streams. In Foster Brook and North Dandalup River, epiphyte area was positively correlated with uncleared cobble treatments, whereas an increase in the variables conductivity, DO and temperature were associated with cobbles in cleared reaches generally. These patterns suggest that the removal of riparian vegetation resulted in a loss of epilithon mass and a slight increase in conductivity, dissolved oxygen and temperature. The composition of epilithon was also related to treatment. Cobbles in cleared reaches generally had either a diatom matrix or no epilithon while cobbles in uncleared reaches were dominated by *Potamogeton ?crispus* and green algae (*Nostoc* type and other chlorophytes).

Discussion

Macroinvertebrate communities of cobbles in cleared reaches had lower macroinvertebrate diversity compared with uncleared controls, which was likely the result of the removal of riparian vegetation. Contributing to the decrease in overall macroinvertebrate diversity was a significant decrease in the abundance of grazers and filterers. This was indicative of a change in the energy base of cobbles, since the composition and biomass of epilithic communities was also altered by clearing. Most cobbles in uncleared reaches supported crops of algae and the angiosperm *Potamogeton*, while most cobbles in cleared reaches were encrusted with a diatomaceous matrix or had essentially no measurable epilithic layer. No difference in any macroinvertebrate community parameter was detected between control and sediment treatment cobbles in the uncleared reaches, suggesting that isolated events involving elevated levels of suspended sediment have little overall effect on the diversity of cobble communities in the short term. This was consistent with the study of Lenat *et al.* (1981), who observed decreases in density but no significant change in community structure of rocky substrates. The effects of elevated sediment on cobble communities might therefore be more important in the longer term and less so than changes in other variables such as accumulations of deposited sediment and others that affect the epilithon.

The magnitude of changes for physical variables such as conductivity, DO and temperature was generally small and no firm conclusions about the relationship between the diversity of fauna and physical variables can be made. There was also no significant increase in nutrient inputs as a result of clearing. Increased nutrient input has been associated with riparian removal in other studies with the consequence of marked changes in ecosystem function (see Lake & Marchant 1990). In a cleared pasture stream, Mosisch *et al.* (1999) reported increased nutrients (mainly nitrogen) to be more important in promoting the growth of epilithic algae than light, although filamentous algae have higher light requirements than unicellular microalgae (Richardson *et al.* 1983; Langdon 1998; Hill 1996). The results of the present study are not surprising, however, given poor nutrient status of jarrah forest soils (Bunn & Davies 1990) and the short (<1 km) length of the cleared reach.

The sediment addition treatment in this study was designed to mimic elevated turbidity levels in the water column that would be expected during heavy rains in the catchment when unconsolidated soils washed into streams (pers. obs.). Several elevations of turbidity over a number of days may have a greater effect on cobble communities than the single addition performed for this treatment. Other factors such as the long term effect of deposited sediment on or around cobbles may also be partly responsible for the differences observed between impact and control cobble communities. For example, in the long term, decomposition of compounds associated with materials in the bedload may depress pH and eliminate acid-sensitive species of Plecoptera and Ephemeroptera (Lemly, 1982).

Cobbles are not exposed to sediment deposition to the same extent as the surrounding substrate, however, increases in bedload transport and sediment deposition from the water column have the effect of sealing or smothering microhabitats of zero water velocity at rock-water interfaces at the edges of, or behind cobbles (McClelland & Brüsven 1980). The present study was designed to detect possible changes in the macroinvertebrate community due to elevated turbidity, but might also be used to detect the effects of short-term sediment deposition on and around cobbles since it was observed that sand from the added sediment was deposited from the water column in these areas. A greater period of time between sediment addition and sampling may have allowed some individuals to either detach from, or crawl onto the cobble substrate from surrounding microhabitats. Gazey (1994) found that the ephemeropterans *Neboissophlebia occidentalis*, *Nyungara bunni* and *Bibulmena kadjina*, and the trichopteran *Smicrophylax australica* began to drift in significant numbers 3–24 hours after experimental sediment addition due to the effects of deposited sediment rather than elevated turbidity, and therefore, effects in the present study may be delayed. Campbell and Doeg (1989) noted that deposited rather than suspended sediment may be more important in reorganising community structure because the effects may be long term if water discharge during spates is not sufficient to cleanse the substrate. Deposition of suspended solids occurs in streams where boundary friction slows the current, however, it is only in low velocity areas that deposits form and elsewhere the sediment is deposited and resuspended at greater rates.

The results from this study suggest that changes in the composition of the epilithic community were the

main cause of changes in the composition of the macroinvertebrate community. Most cobble substrates in uncleared reaches supported a growth of the aquatic plant, *Potamogeton ?crispus.*, which extended the height of roughness projection of the cobble and provided a relatively complex microhabitat. The epilithon on cleared cobble substrates did not support the same microhabitat. The microhabitat amongst the epilithon may have provided protection in the short-term from elevated turbidity levels by allowing fauna to avoid any adverse effects such as the clogging of respiratory or food capturing devices. These fauna may have otherwise responded by drifting. Such effects were identified by Lemly (1982) as being the result of long term bedload transport on filtering species, and refuge-seeking behaviour was one of the strategies employed by some macroinvertebrate species in a New Zealand braided stream which was exposed to periodic flood events (Scrimgeour & Winterbourn, 1989).

The loss of *Potamogeton ?crispus* in cleared reaches might be attributable to increased light availability. Limitation in growth and survival of epilithon communities after an increase in sediment levels has also been documented previously (silt accumulation, Graham 1990; sediment abrasion, Lewis 1973a,b). Generally, it appears that shading limits the growth of larger algal forms, with algal assemblages in shaded areas being dominated by diatoms (Duncan & Blinn 1989). When light levels are increased, a greater biomass of green and blue-green algae results, with the growth of diatoms being inhibited by high light conditions (Hill & Knight 1988; Steinman *et al.* 1989; Wellnitz *et al.* 1996). Loss of riparian vegetation in other Australian ecosystems also resulted in a decline in the health of forest streams, and instream primary producers shifted from unicellular algae to filamentous green algae and macrophytes (Bunn *et al.* 1999a). However, there are exceptions to this pattern. In a subtropical stream surrounded by pasture, diffusion surfaces exposed to full sunlight were dominated by diatoms (Mosisch *et al.* 1999), and a layer of diatoms and filamentous algae was present on cobbles in a braided stream in New Zealand, the outcome of scouring and rolling (Scrimgeour & Winterbourn 1989). The cobble epilithon of the jarrah forest streams of the present study resembled the latter unshaded streams.

In Australian tropical and subtropical streams, the epilithic unicellular algae contributes to the majority of consumption by macroinvertebrates on cobbles, but in the northern jarrah forest unicellular algae contributes little more than 50 % of carbon assimilated by cobble fauna (Bunn *et al.* 1999a). Jarrah forest stream ecosystems are almost entirely dependent on terrestrial sources of carbon (Davies 1994; Bunn *et al.* 1999a) and there is a corresponding low diversity of algal grazers (Bunn & Davies 1990). This suggests that measuring only the change in abundance of grazers on cobbles does not have the same utility in the jarrah forest than other stream ecosystems for detecting effects of disturbances. However, the present study has shown that measures of overall macroinvertebrate diversity on cobbles are useful for detecting changes in ecosystem health, and grazers, while making up only part of the community, showed the same response. Furthermore, a simpler measure of the change in macroinvertebrate community structure

would be indicated by obvious changes in the epilithon of cobbles.

Despite previous studies of northern jarrah forest streams that have shown communities within the same stream order to be generally homogeneous (Storey *et al.* 1990), differences in some macroinvertebrate parameters were found between streams. This was probably due to the differences in epilithon cover between streams. Lush growths of *Potamogeton* sp. were not present on every cobble in uncleared reaches, and although not tested in the present study, the variability in epilithic cover in uncleared reaches between streams may have contributed to the variation in macroinvertebrate communities between streams. Cobbles in jarrah forest streams may therefore be more heterogeneous than previously reported (Davies 1994) and this would be a consideration when using cobbles as an indicator habitat for assessing changes in stream ecosystem function.

Changes in chironomid community structure, as observed in the present study, is often used as an indicator of change in the stream ecosystem (Storey & Edward 1989, Smith & Cranston 1994, Edward *et al.* 2000). Other species might have some use in this regard. A number of the taxa on impact cobbles were unique to this treatment, although the proportion of unique taxa in uncleared areas was greater. Species unique to cleared cobble communities included the simuliid *Cnephia tonnoiri* and the coleopterans *Hyphydrus sp.* and *Psychodidae sp.*, however, they were relatively uncommon and therefore may need to be used in conjunction with other indicators such as changes in epilithon. Unique taxa may be present on cleared cobbles for one of two reasons. Firstly, they could be relatively rare and therefore collected by chance alone, or secondly, some species such as the water beetle *Sternopriscus marginata* may have preferred other stream meso-habitats prior to clearing, but increased in numbers in cobble habitats as they became more favourable in some respect.

In conclusion, complete removal of riparian vegetation adversely affects biodiversity and composition of macroinvertebrate fauna and epilithic vegetation on cobbles. The most important changes are likely to include reduced bank stability, and increased light and sediment levels. Short-term increases in suspended sediment levels appear to have minimal effect, but the longer term effect, coupled with that of sediment deposition could be greater. Cobble communities as a whole are sensitive to changes in the aquatic ecosystem and are recommended for use when assessments of ecosystem health are being made. The most useful indicator of changes in ecosystem health may be the change in composition and biomass of epilithon. In the jarrah forest, clearing causes a general change from *Potamogeton ?crispus* to diatomaceous layers. Removal of riparian vegetation is not recommended if aquatic biodiversity and normal ecosystem functioning is to be maintained. This has implications in the south-west of Western Australia for logging practices, whereby streamside vegetation should be maintained on all streamlines.

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Stylidium validum (Stylidiaceae): a new trigger plant from southern Western Australia

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Abstract

A new southern Western Australian endemic trigger plant, *Stylidium validum* Wege, is described as part of a broader taxonomic research project. *Stylidium validum* is characterised by a robust, caespitose habit, a tufted basal rosette of glaucous, oblanceolate leaves, a glabrous scape axis, an ellipsoid, glandular hypanthium, and laterally-paired corolla lobes that are white to pale pink-mauve with two sets of throat markings. This species has conservation priority since it is known from only three locations within the South-western Interzone, west of Norseman. Illustrations and a distribution map are provided.

Keywords: taxonomy, *Stylidium*, greenstone

Introduction

The trigger plant genus *Stylidium* (Stylidiaceae) comprises over 240 taxa characterised by a touch-sensitive floral column that places pollen on, or removes pollen from an insect's body. Approximately 70% of taxa are endemic to the south-west of Western Australia (Wagstaff & Wege 2002). Within this region, centres of species richness in the genus are higher close to the coast, especially in the high rainfall zone (Burbidge 1984). Far fewer species occur in the drier, South-western Interzone (or Coolgardie bioregion). Here, species of *Stylidium* are known from seepage zones adjacent to granite outcrops (e.g. *S. dielsianum* E. Pritz.), areas of sandplain (e.g. *S. choreanthum* F.L. Erickson & J.H. Willis, *S. limbatum* F.Muell., *S. arenicola* Carlquist) and adjacent to salt lakes systems (e.g. *S. pulviniforme* Lowrie & Kenneally).

Examination of the herbarium collection at The Western Australian Herbarium (PERTH) uncovered specimens of *Stylidium* from the South-western Interzone not referable to any known taxon. Subsequent field searches relocated this entity and confirmed it to be a distinct new species. A description, illustration and distribution map are provided herein. This research forms part of a wider treatment of *Stylidium* for the Flora of Australia.

Methods

This study is based on herbarium specimens housed at PERTH and The National Herbarium of Victoria (MEL), and on the field observations of the author. Morphological characters were coded using a combination of fresh, spirit and herbarium material. Corolla lobe measurements were based solely on material collected from the type locality (*JAW 982*) and preserved in 70% ethanol. Trichomes from the spirit collection were cleared in domestic bleach and mounted in Apathy's Aqueous Mountant for examination under a compound microscope.

Data were recorded as a DELTA dataset (Dallwitz *et al.* 1993) from which a species description was generated. The distribution map was compiled using Online Map Creation (OMC) and is based on PERTH specimen data.

Taxonomy

Stylidium validum Wege *sp. nov.*

Species haec ab *Stylidio turleyae* Lowrie & Kenneally differt scapo glabero et glauco, foliis ad 6 mm latis, pagina abaxiali corollae immaculata.

Typus: Forrestiana – Southern Cross Road, N of Hyden – Norseman Road [precise locality withheld for conservation purposes], 17.x.2003, *J.A. Wege and C. Wilkins JAW 982* (holo: PERTH 06815502; iso: CANB, K, MEL, W).

Caespitose perennial herb 11–50 cm high. Stem stock compact and part-buried, rarely shortly elongated. *Glandular trichomes* restricted to the inflorescence branches, 0.1–0.3 mm long; stalks multicellular, biseriate, translucent; heads red, ellipsoid, multicellular. *Eglandular trichomes* present in the leaf axils, *c.* 3–4 mm long, multicellular, uniseriate, cells cylindrical. *Leaves* arranged in a basal tuft, bluish-green (glaucous) tinged red at apex, oblanceolate, flattened in cross section, apex acute to acuminate, margin entire, 1.5–10 cm long, 2–6 mm wide, glabrous. *Scapes* 9–50 cm high, 0.7–3 mm wide, axis glabrous and glaucous. *Inflorescence c.*15-115-flowered, paniculate; branches glandular, 2-19-flowered, 1.5–13 cm long. *Bracts* and *bracteoles* green with red tips, lanceolate to linear-lanceolate, apex acute, margin entire; bracts 2–10 mm long, 1–2 mm wide, glabrous; bracteoles 1.5–5 mm long, glabrous or sparingly glandular at base. *Pedicels* 1.5–6 mm long, glandular. *Hypanthium* ellipsoid, 2–4 mm long, 1.2–2.1 mm wide, glandular. *Calyx lobes* green with red tips, free, apex subacute to acute, margin entire, 1.8–2.3 mm long, 0.8–1.2 mm wide, glabrous or
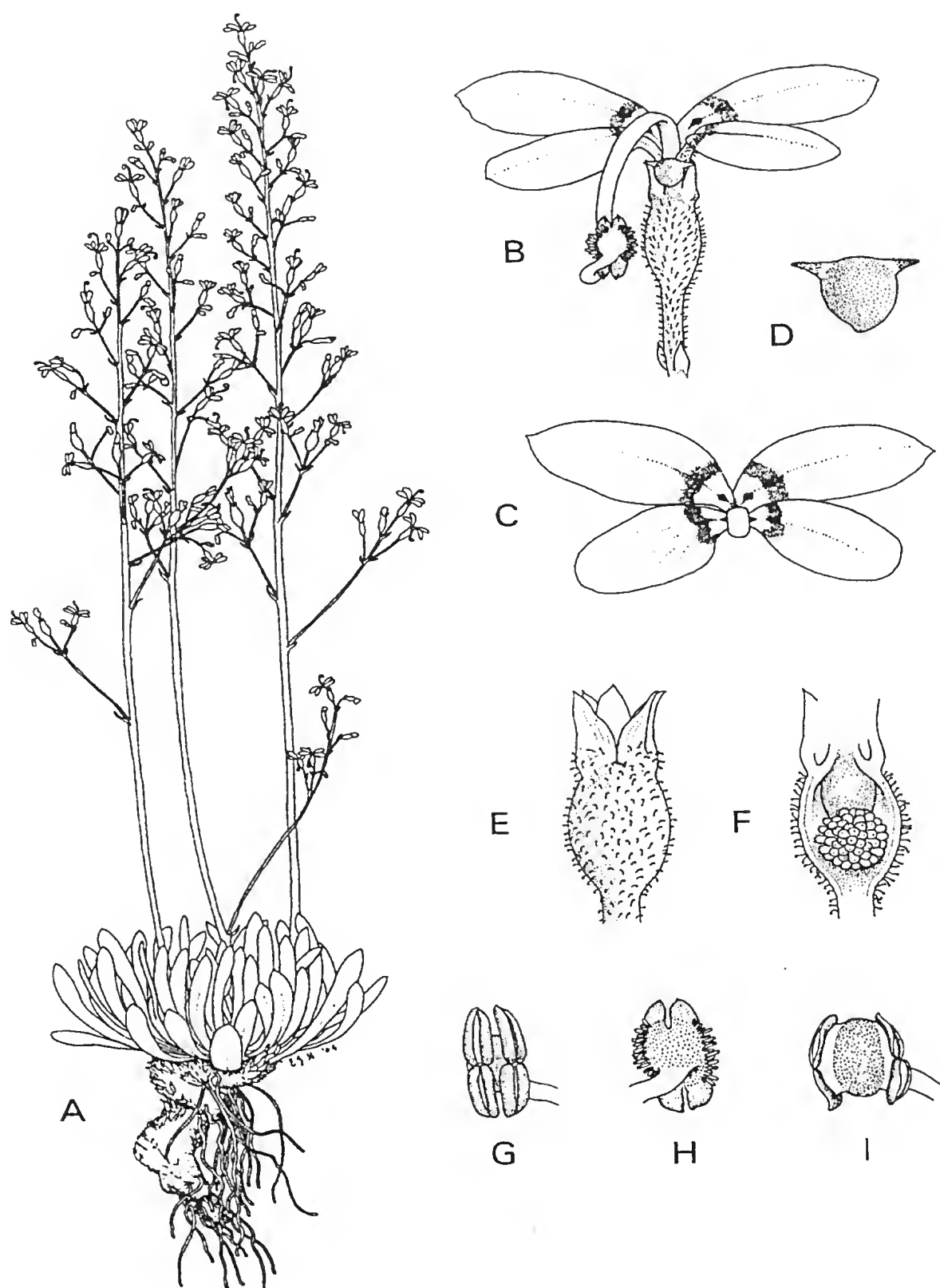
Figure 1. *Stylidium validum* (*JAW 982*). A, habit x0.5; B, flower x5; C, corolla lobes x5; D, labellum x10; E, hypanthium x7.5; F, L.S. through hypanthium x7.5; G, anthers x8.75; H, column apex showing subtending anther hairs x8.75; I, stigma x8.75. Illustration by Ellen Hickman.
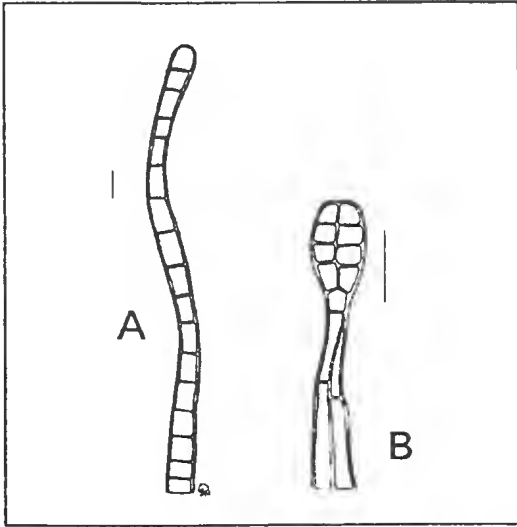
Figure 2. Trichome structure in *Stylidium validum* (*JAW 982*). A, eglandular trichome (leaf axil); B, glandular trichome (inflorescence). Scale bars at 50 μm.

sparsely glandular at base. *Corolla* white to pale mauve-pink or pink with prominent mauve-pink external throat markings and smaller inner red markings, throat white; abaxial surface white, glandular; tube 2–3 mm long; lobes laterally-paired, elliptic; anterior lobes 4.5–5.7 mm long, 2.8–3.3 mm wide; posterior lobes 5.5–7.5 mm long, 3–3.8 mm wide. *Labellum* boss yellow with a pink papillose margin, orbicular to broadly ovate, 0.9–1.5 mm long, 0.8–1.4 mm wide; lateral appendages pink or yellow with pink tips, 0.3–0.7 mm long. *Throat appendages* absent. *Column* 11.5–13.7 mm long, glabrous. *Anther locules* black, obliquely angled relative to column, subtending hairs translucent, pollen yellow. *Stigma* sessile, entire, cushion-like. *Capsule* ellipsoid, *c*. 6.5–8 mm long. *Seed* not viewed. Figs 1–2.

Other specimens examined [precise localities have been withheld for conservation purposes]. WESTERN AUSTRALIA: New Norseman – Hyden Track, 28.ix.1999, *B. Archer 1379* (MEL, PERTH); N of Lake Johnson turn-off on Lake King – Southern Cross Road, 25.ix.1971, *C.I. Stacey 66* (PERTH); Bremer Range, 19.ix.1994, *N. Gibson & M. Lyons 2360* (PERTH).

Phenology. Flowering specimens are known from late September and October.

Etymology. The species epithet is taken from the Latin (*validus* – robust, stout) and refers to the sturdy habit of this species.

Distribution and habitat. Stylidium validum is found between Norseman and the Forrestiana – Southern Cross Road (Fig 3) where it occurs in upland, ironstone and greenstone habitats bearing low sclerophyll woodland.

Conservation Status. Conservation Codes for Western Australia Flora: Priority 1. *Stylidium validum* has not been recorded within a conservation reserve and population numbers at each of the known locations appear low. Immediate surveys are recommended given the prevalence of mineral exploration activity in the Forrestiana and Bremer Range regions.

Affinities. Stylidium validum is cautiously aligned here to *S. turleyae* Lowrie & Kenneally. This trigger plant, recently described by Lowrie & Kenneally (2004), possesses a comparable habit, inflorescence structure and leaf margin to that of *S. validum*. The flowers of both taxa are also very similar: the corolla lobes are elliptic, bear two sets of throat markings, and lack throat appendages. *Stylidium turleyae* differs most obviously in possessing glandular scapes, narrower leaves and prominent dark pink markings on the abaxial surface of the corolla. Furthermore, *Stylidium turleyae* has a more southerly distribution, with populations scattered across the south coast from near Israelite Bay west to Fitzgerald River
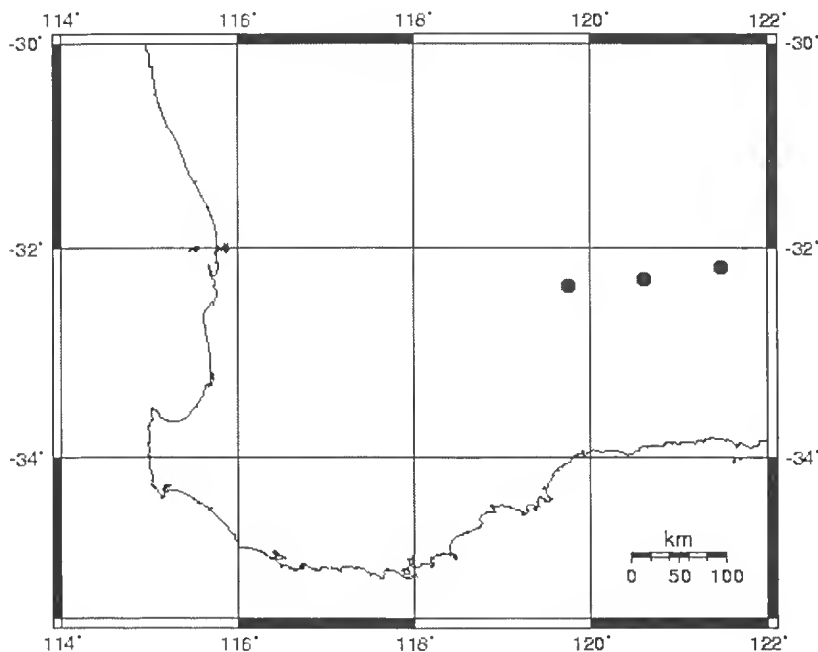
Figure 3. Distribution of *Stylidium validum.*

National Park. It grows in sandy habitats, often in winter-wet localities, rather than on rocky substrates in upland habitats like *S. validum*. Different habitat preferences are often a feature of species differentiation in *Stylidium* (Carlquist 1969; Carlquist 1976; Coates 1982; Wege 2005a).

Stylidium validum is also likely to be confused with *S. limbatum* since these two species possess a comparable habit, inflorescence structure and flower morphology, and have overlapping distributions. *Stylidium limbatum* can be readily differentiated by its densely glandular scape, conspicuous hyaline leaf margin, prominent apical leaf mucro and sandy habitat preference.

Classification. The most recent classification of *Stylidium* is that of the German botanist Mildbraed (1908). Whilst the genus has more than doubled in size since this time, a more up-to-date system is not presently available. On the basis of habit, floral morphology and glandular trichome structure, both *S. validum* and *S. turleyae* are currently best placed in subgenus *Nitrangium* (Endl.) Mildbr. and allied to the basally-tufted species within section *Thyrsiformae* (Benth.) Mildbr. until a formal revision of the infrageneric taxonomy of *Stylidium* is completed.

Rust. The rust pathogen *Puccinia stylidii* McAlpine has been recorded on several species of *Stylidium* (Wege 2005b). *Stylidium validum* and *S. turleyae* can be added to the list of known hosts. In both cases the rust is largely restricted to the leaves and does not appear to have a detrimental impact on overall plant health or reproductive capacity. It is not known how many trigger plants are susceptible to infection by this pathogen.

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Wege J A 2005b Reinstatement of *Stylidium rigidulum* (Stylidiaceae), with notes on the morphologically allied *S. kalbarriense*. Nuytsia (in press).

Burrows of desert-adapted frogs, *Neobatrachus aquilonius* and *Notaden nichollsi*

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Abstract

The non-cocooning frogs, *Notaden nichollsi* and *Uperoleia micromeles*, and the cocoon-forming frog, *Neobatrachus aquilonius*, burrow underground to survive in the hot, dehydrating arid interior of Australia. By four to six months after these frogs had burrowed, the only surface evidence that a frog had dug a vertical burrow was either a small raised-side crater ranging from 50 – 60 mm in diameter or a shallow depression the same size with a less compacted centre. *Notaden nichollsi* and *U. micromeles* were dug from poorly-defined, sand-filled burrows in sandy soil (1.4 – 4.1% clay and silt, 95.9 – 98.4% sand) at 600 to 2400 mm below the surface. Multiple *N. nichollsi* and *U. micromeles* were located in single burrows. In contrast, *N. aquilonius* were found in clay soil (12.5 – 17.9% clay and silt, 82.1 – 87.5% sand) in burrows 280 to 1200 mm deep. At a clay pan site only a single *N. aquilonius* was found in each well-defined, loosely filled burrow that we excavated. From a swale site, on one occasion we found two *N. aquilonius* in one burrow, and on another occasion we found a *N. aquilonius* and a *N. nichollsi* in the same burrow.

Keywords: frogs, arid, micro-habitat, Australia

Introduction

Arid-adapted frogs are abundant in many locations in the interior of Australia (Predavec & Dickman 1993; Morton *et al.* 1993). Despite this abundance we know little of the life history and ecology of these frogs. However, in recent years there has been a growing appreciation of the physiological and anatomical adaptations that enable some frog species to flourish in arid environments (Main & Bentley 1964; van Beurden 1977; 1982; 1980; 1984; Withers 1993; 1995; 1998; Withers & Thompson 2000; Bayomy *et al.* 2001). Most of what is known comes from laboratory experiments and indicates that there are two basic strategies to survive dehydrating arid environments. One group (including all *Cyclorana* spp. and *Neobatrachus* spp.) form a cocoon by continuously shedding multiple layers of skin (Withers 1995) and life underground is prolonged appreciably by a reduction of metabolic rate (Withers 1993) and tolerating dehydration (Main & Bentley 1964). An alternative strategy is to dig deep into the substrate but not to form a cocoon (including *Notaden* spp. and *Uperoleia* spp.). Much less is known about this latter group's anatomical, physiological and behavioural adaptations to their potentially dehydrating environment.

When frogs are surface-active following rain, it is often difficult to access their habitat due to local flooding and the impassable condition of unsealed roads. In addition, locating frog burrows during extended dry periods is also difficult for the untrained observer and the task of excavating them can be arduous. There are only three brief reports on the burrows and microhabitats selected by arid-adapted Australian frogs (Slater & Main 1963; van Beurden 1984; Paltridge & Nano 2001).

During a field trip to the Kiwirrkurra Community in the Gibson Desert, Aboriginal women dug up a *N. nichollsi* from near the base of a sand ridge, many months after the last rain. We subsequently returned to Kiwirrkurra to draw on Aboriginal knowledge of arid-adapted frogs during June 2003 and again in September 2004. Our specific objective was to locate burrows and excavate frogs for the purpose of describing their microhabitat as they lay dormant underground.

Methods

During late June 2003, Aboriginals from the Kiwirrkurra Community (22° 49' S, 127° 47' E) took us to three locations for the specific purpose of locating *N. nichollsi* and *N. aquilonius*. We dug 22 frogs from burrows (a tunnel created by a frog that was loosely, passively filled with soil); six *N. aquilonius* and 16 *N. nichollsi*. We returned in September 2004, revisited these three sites and an additional two locations, and dug up another nine *N. aquilonius* and 12 *N. nichollsi*.

We recorded the surface habitat at the five sites (sites 1 and 2 were on sand ridges, site 3 was a clay pan, site 4 was a swale, and site 5 was the edge of dry creek bed) where burrowed frogs were excavated, and measured the depth of the frog below the surface. To quantify the difference in soil type between sites, soil samples were

taken from burrows adjacent to where we located three *N. aquilonius*, three *N. nichollsi* and a burrow in which we found a *N. aquilonius* and a *N. nichollsi*, and were used for soil particle size analysis (see Gilkes *et al.* 2000 for methods). Our analysis measured the proportion of sand, silt and clay in the substrate, which affects soil water retention properties and is particularly relevant to burrowed frogs. Soil temperature was measured at various depths by inserting a probe from a digital thermometer approximately 60 mm horizontally into the soil profile at various depths in the hole dug to retrieve the frog. Soil temperature profiles were taken for most burrows.

For *N. aquilonius* burrows, we either left the burrow intact, and dug around the hole (Plate 3), or dug down one side of the burrow, which enabled us to check for side burrows. Compaction of soil within the burrow was much less than for the adjacent soil, so it was easy to excavate the burrow and confirm the absence of side burrows. For *N. nichollsi*, we dug from one side of the loose, sand-filled burrow, leaving a semi-circular burrow evident on the unexcavated side (see Plate 7). The less compacted soil in the burrow made it relatively easy to excavate down a burrow.

We collected *N. nichollsi* that were surface active one night by searching with head torches.

Results

Residents at Kiwirrkurra indicated that the most recent heavy rain prior to our visit in June 2003 was in November 2002, and for our September 2004 visit, the most recent heavy rain had been during March 2004, so we estimated that about five months in 2003 and about six months in 2004 had elapsed since the frogs had burrowed.

Frogs were located at five different locations; two of these were sand ridges (sites 1 and 2), a clay pan (site 3), a swale (site 4), and the edge of a dry creek bed (site 5).

Neobatrachus aquilonius burrows

Fifteen *N. aquilonius* were excavated, with a mean snout-to-vent length of 40.0 (±se 0.14) mm and a mean body mass of 10.2 (±se 0.10) g. We found seven *N. aquilonius* in a clay pan (site 3; 22° 58' S 127° 54' E) that was sparsely vegetated with scattered mulga trees, tufts of grass and many large bare patches (Table 1; Plate 1). It had been burnt just before our 2004 visit and most of the ground litter and grass had been reduced to ash. Ash covered much of the ground which made it difficult to locate frog burrows. We excavated seven *N. aquilonius* in a swale (site 4; 22° 57' S 127° 53' E), which was about 200 m from a 7 m high red sand ridge. The swale was vegetated with groups of small trees, scattered shrubs, spinifex and the occasional Desert Oak. One *N. aquilonius* was excavated adjacent to Walla Walla Creek (site 5; 22°

54' 127° 40' E), which was a dry creek bed with steep sides (0.8 – 1.1 m).

Rain and wind damaged craters (Plate 2) or shallow depressions indicated where *N. aquilonius* had burrowed into the ground. Each crater or depression ranged in diameter from 50 – 60 mm. Burrows were vertical and the soil in each burrow was much less compacted than the surrounding soil. We either excavated each frog by digging adjacent to, or around the burrow, so as to not disturb or damage the frog when we eventually reached it (Plate 3).

The depth of the 15 *N. aquilonius* below the surface ranged from 280 to 1260 mm (Table 1). The maximum depth of the burrow was 750 mm in the clay pan, but *N. aquilonius* had deeper burrows in the less compacted soil of the swale (down to 1260 mm). There was no enlargement at the base of the burrows where *N. aquilonius* were located (Plate 3). Each burrow was filled with soil and each frog was in close contact with the loosely compacted soil at the bottom of their burrow. When a hole is dug adjacent to a burrow, the loosely compacted soil fell freely out of the hole, revealing its size and shape (Plate 3).

The clay pan (site 3) and the swale (site 4) had relatively high proportions of silt and clay (12.5 – 17.9% clay and silt, 82.1 – 87.5% sand) and were classified as 'clayey soils' (Table 2). Soil surrounding *N. aquilonius* burrows in the clay pan was much more compacted and difficult to dig in than in the swale. At Walla Walla Creek, the surface soil layer was a course sand over a deeper layer of coarser gravel. Surface soil temperature varied according to the time of the day it was measured. The clay pan (site 3) soil temperature ranged from 19 to 24 °C in June 2003 from 50 to 700 mm below the surface and it was about five °C higher in September 2004 (Fig. 1). Soil temperature in the swale (site 4) in September 2004 ranged from 25 – 27 °C from 20 to 120 mm below the surface (Fig. 1).

All *N. aquilonius* excavated at the clay pan (site 3) in 2003 and 2004 had a well developed cocoon that was thick enough for it to retain the shape of the frog after it was carefully removed (Plate 4). *Neobatrachus aquilonius* unearthered in the swale (site 4) and at Walla Walla Creek (site 5) in 2004 had very thin and flimsy layers of shed skin that were difficult to detect and which did not constitute a cocoon.

Notaden nichollsi and Uperoleia micromeles burrows

Twenty eight *N. nichollsi* were excavated at three locations (sites, 1, 2 and 4). Burrows containing *N. nichollsi* were located at the base, the face and on top of sand ridges. One *N. nichollsi* was found in a burrow with a *N. aquilonius*, in a swale about 200 m from the closest sand ridge (site 4). Site 1 (22° 48' S, 127° 48' E) was a red sand ridge adjacent to a swale that contained evidence of a temporary pond after heavy rain. The 5 – 10 m high

Plates. 1 – Clay pan in Mulga habitat typical of where *N. aquilonius* burrows were located; 2 – surface of a *N. aquilonius* burrow approximately five months after it burrowed; 3 – burrow of *N. aquilonius* in compacted clay showing the cocooned frog at the bottom (*n.b.* all the loose soil has run out of the burrow); 4 – cocoon from a *N. aquilonius* removed after approximately 6 months of aestivation; 5 – typical habitat for *N. nichollsi* and *U. micromeles* burrows; 6 – surface evidence of a *N. nichollsi* burrow, 7 – burrow of *N. nichollsi* that has been excavated to show its vertical orientation; 8 – *N. nichollsi* from the Gibson Desert.
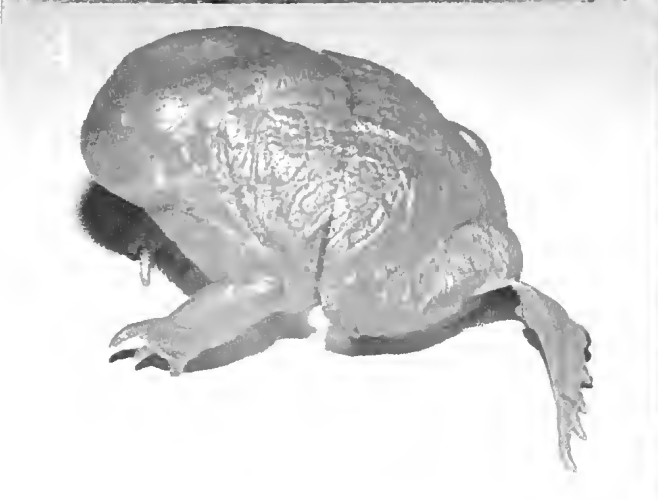
Table 1

Number and depth of burrowed frogs, and surface habitat.

Month / year	Frogs found	No in burrow	Burrow depth (mm) at frog	Site ID	Location	Surface vegetation
Jul-03	N. aquilonius	1	600	Site 3	Clay pan	Tufts of grass, scattered shrubs, scattered Mulga trees
Jul-03	N. aquilonius	1	600	Site 3	Clay pan	Tufts of grass, scattered shrubs, scattered Mulga trees
Jul-03	N. aquilonius	1	600	Site 3	Clay pan	Tufts of grass, scattered shrubs, scattered Mulga trees
Jul-03	N. aquilonius	1	750	Site 3	Clay pan	Tufts of grass, scattered shrubs, scattered Mulga trees
Jul-03	N. aquilonius	1	750	Site 3	Clay pan	Tufts of grass, scattered shrubs, scattered Mulga trees
Jul-03	N. aquilonius	1	280	Site 3	Clay pan	Tufts of grass, scattered shrubs, scattered Mulga trees
Sep-04	N. aquilonius	1	300	Site 3	Clay pan	Tufts of grass, scattered shrubs, scattered Mulga trees
Sep-04	N. aquilonius	1	1200	Site 5	Walla Walla Ck	Under the edge of a large shrub, and tufts of grass
Sep-04	N. aquilonius/ N. nichollsi	2	1120	Site 4	Swale	Scattered shrubs and spinifex
Sep-04	N. aquilonius	1	1260	Site 4	Swale	Scattered shrubs and spinifex
Sep-04	N. aquilonius	2	1100	Site 4	Swale	Scattered shrubs and spinifex
Sep-04	N. aquilonius	1	1200	Site 4	Swale	Scattered shrubs and spinifex
Sep-04	N. aquilonius	1	1100	Site 4	Swale	Scattered shrubs and spinifex
Sep-04	N. aquilonius	1	1000	Site 4	Swale	Scattered shrubs and spinifex
Jul-03	N. nichollsi	4	700	Site 1	Top of sand ridge	Scattered shrubs to 1.2 m, hole next to grass tufts, but exposed
Jul-03	N. nichollsi	1	700		Top of sand ridge	As above, burrows were about 100 mm apart
Jul-03	N. nichollsi	3	700	Site 2	Base of dune	Scattered shrubs to 1.2 m, scattered grasses and spinifex, hole under a low shrub
Jul-03	N. nichollsi	1	1600	Site 2	Two thirds the way up a sand ridge	Scattered shrubs and spinifex, hole found under over hanging Acacia branches
Jul-03	N. nichollsi	7	2400	Site 2	One third the way up a sand ridge	Scattered shrubs and spinifex, burrow in an exposed location
Jul-03	U. micromeles	2		Site 2		Same hole as above
Sep-04	N. nichollsi	1	730	Site 2	Two thirds the way up a sand ridge	Scattered shrubs and spinifex
Sep-04	N. nichollsi	1	1060	Site 2	Mid way up a sand ridge	Scattered shrubs and spinifex, burrow in an exposed position.
Sep-04	N. nichollsi	3	1450	Site 2	Top of sand ridge	Burrow in an exposed location
Sep-04	U. micromeles	3	750, 1000, 1450	Site 2	Top of sand ridge	Same hole as above
Sep-04	N. nichollsi	4	1530, 1530	Site 2	Top of sand ridge	Burrow in an exposed location
Sep-04	U. micromeles	2	1200, 1530	Site 2		Same hole as above
Sep-04	N. nichollsi	1	1000	Site 2	Top of sand ridge	Burrow in an exposed location
Sep-04	N. nichollsi	1	600	Site 2	Top of sand ridge	Burrow in an exposed location

Table 2

Composition of the soil from adjacent to Neobatrachus aquilonius and Notaden nichollsi when located in burrows. Mean ±1 se in parenthesis; n = 3 for each cell.

Soil component	N. aquilonius burrows – clay soils			N. nichollsi burrows – sandy soils			N. aquilonius / N. nichollsi burrow
	Site 3	Site 3	Site 3	Site 1	Site 2	Site 2	Site 4
% clay and silt	13.0 (0.09)	17.9 (1.09)	12.5	1.6 (0.96)	3.4 (0.06)	4.1 (0.57)	14.2
% sand	87.0 (0.91)	82.1 (1.09)	87.5	98.4 (0.96)	96.6 (0.06)	95.9 (0.57)	85.8
Depth (mm) at which the frog was found and the soil samples were taken	1260	600	280	700	700	2400	1120
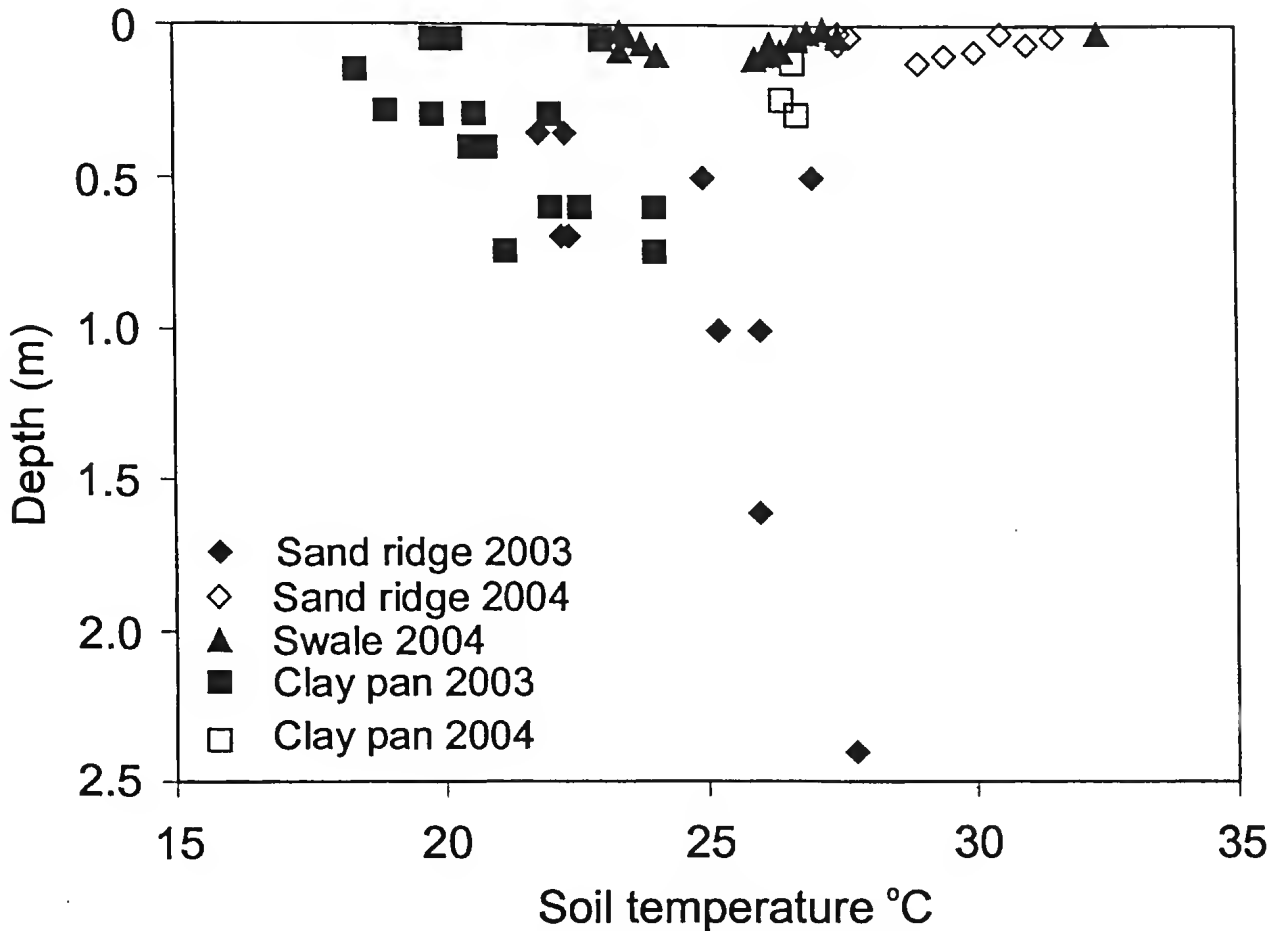
Figure 1. Soil temperature (°C) at various depths in sand dunes, the burrow location of *N. nichollsi*, a clay pan and a swale, the burrow location for *N. aquilonius*

sand ridge was covered with scattered shrubs to 1.2 m, spinifex, tufts of grass and the occasional small tree (Plate 5). Site 2 (22° 49' S, 127° 34' E), where we caught *N. nichollsi* and *U. micromeles*, was the side and top of a red sand ridge between two swales that contained surface water after heavy rain. The sand ridge was covered with spinifex, scattered shrubs to about 1.5 m and tufts of grass. The sand ridge was approximately 12 m high and formed a crescent around one of the swales.

At the surface, some burrows had slightly-raised sides forming a small crater (Plate 6) whereas others had a nearly circular depression. The diameter of craters and depressions ranged from 50 – 60 mm. All burrows were vertical with no side burrows and were loosely filled with sand. The less compacted sand of the burrow guided excavation as we could feel with our fingers where the sand had been previously disturbed (Plate 7). The loose compaction of sand around *N. nichollsi* (which was less noticeable than for *N. aquilonius*) made it difficult to determine whether there was an enlarged, air-filled chamber around each frog; if there was, it was small and not obvious. *Notaden nichollsi* were located between 600 mm and 2400 mm below the surface.

Uperoleia micromeles were located in the same burrow as *N. nichollsi* on three occasions, but they were never found at the bottom of the burrow.

Sand ridge sites (1 and 2) had a low silt and clay

content (1.4 – 4.1% clay and silt, 95.9 – 98.4% sand) and were classified as 'sandy soils' (Table 2). Soil temperature in June 2003 in the sandy ridges increased from about 20 °C at 50 mm to about 28 °C at 2400 mm below the surface (Fig. 1). In September 2004, soil temperatures at these sites were generally higher (27 – 31 °C from 20 to 1500 mm below the surface).

At the conclusion of a morning excavating frogs, our Aboriginal guides pointed out *N. nichollsi* tracks on the top of the sand ridge at site 2. The previous night had a higher than normal humidity (due to the dense cloud cover) but there was no evidence that it had rained (e.g. rain drop marks on the soil). That afternoon the area had a light shower of rain, sufficient to cover the surface (≈ 3 mm). After it rained the clouds cleared and the sun evaporated any obvious surface moisture (i.e. the sand was dry to touch). We returned to site 2 that night and collected 17 *N. nichollsi* foraging on the top and sides of the sand ridge. It was not raining and the soil surface was not damp. The ambient temperature in the afternoon had been in the low 30s °C.

Notaden nichollsi that we excavated had significantly longer snout-to-vent lengths (SVL) and a higher body mass than those caught foraging (excavated frogs: mean SVL 45.6 (±se 1.97) mm, 14.3 (±se 1.15) g; foraging frogs 38.5 (±se 2.17) mm, 8.5 (±se 0.83) g, t_{27} = 3.3, $P < 0.05$ for SVL, t_{27} = 2.48, $P < 0.05$ for mass).

Discussion

In general, habitats selected by *N. nichollsi* and *N. aquilonius* were very different. Our Aboriginal advisers indicated that *N. nichollsi* and *U. micromeles* were always found near red sand ridges, adjacent to swales that had contained temporary ponds after heavy rain, whereas *N. aquilonius* were in clay soils that were sparsely vegetated with mulga trees and tufts of various grasses. We also found *N. aquilonius* in a swale about 200 m from a sand ridge. Soil particle size analysis indicated that the non-cocooning *N. nichollsi* were found in sandy soils, whereas the cocoon-forming *N. aquilonius* were generally in clay soils (Table 2). Three *N. aquilonius* burrows at the clay pan (site 3) were within 1 m of a small mulga tree (site 3), but the others were more distant. Burrows of *N. aquilonius* on the swale did not seem to be located in any particular place (e.g. under a shrub, near trees, adjacent to spinifex).

Slater & Main (1963) reported finding *N. nichollsi* and *U. mjobergi* in the same burrows, and Paltridge & Nano (2001) reported finding multiple *U. micromeles* and *N. nichollsi* in the same sand-filled burrows. We also observed this genus association for three of our excavated burrows. Presuming that it is *N. nichollsi* that actually digs the burrow, it appears that both *Uperoleia micromeles* and *U. mjobergi* are able to locate and dig into the burrows of *N. nichollsi*. Whether this occurs at the time that *Notaden* dig the burrow, or sometime after it has been dug, is not apparent.

Non-cocooning frogs (*N. nichollsi* and *U. micromeles*) presumably have a capacity to move underground should the soil conditions become unsuitable, but we found only vertical burrows and no evidence of lateral movement, even when there was more than one frog in the burrow. Side tunnels would have been easy to detect as the soil compaction in these burrows would have been less than in the surrounding soil. In one burrow, not all the *N. nichollsi* were at the bottom, and *U. micromeles* were never found at the bottom of burrows. Slater & Main (1963) also reported that *U. mjobergi*, in the burrows with *N. nichollsi*, were not located at the bottom. We presume that *N. nichollsi* dug to a particular depth to gain access to moisture. If this is the case, then the reason why all frogs were not at the bottom of the burrow is not clear, as presumably the water management requirements of each species would be similar.

We were very surprised to find that *N. nichollsi* had emerged and were foraging in the evening when there had been no overnight rain and only a small quantity of afternoon rain. This small quantity of rain presumably would not have penetrated more than a couple of mm into the soil and most would have evaporated soon after the rain clouds had passed. The environmental cue(s) for emergence of *N. nichollsi* is not known. If *N. nichollsi* emerge infrequently to forage on humid nights, then they could replenish their energy stores by feeding, and replenish their water stores while underground (Lee 1968). Cocooning species reduce their metabolic rate once the cocoon forms (Withers 1995), prolonging the period they can remain dormant underground. It is not known if there is a similar reduction in the metabolic rate by *N. nichollsi* when they remain underground for an extended period, as occurs in *Scaphiopus* (Seymour 1973). If these

non-cocoon forming species do not reduce their metabolic rate, then they may be compelled to forage at the surface when conditions permit, and this may mean foraging on humid nights and when there has been little or no rain. If they do metabolically depress, then surface foraging during favourable conditions would further extend their survival period but would interrupt their metabolic depression and would incur an energy cost as frogs return to a depressed metabolic state over a number of weeks (Withers 1995).

It is likely that foraging under the conditions that we encountered *N. nichollsi* would cause them to dehydrate rapidly and there would be a significant cost associated with again burrowing to a depth that would enable them to achieve water balance (unpublished data). The activity patterns and associated energetics of *N. nichollsi* therefore appear to be a fertile area for future research.

As *N. aquilonius* form a cocoon at the bottom of their burrows they can not move underground to more favourable locations. Their inability to move once a cocoon has formed is probably not important as the cocoon significantly reduces water loss across the skin (the mouth and cloaca are sealed shut by the cocoon). We were very surprised to find a number of burrowed *N. aquilonius* at site 3 that had only a few layers of 'flimsy' shed skin indicating that cocoon formation had just commenced. If these frogs had burrowed soon after the heavy rains in March 2004, as was expected, and cocoon formation was at the rate reported by Withers (1995), then well-formed cocoons should have been evident. If the reason for the few layers of shed skin instead of a cocoon was that the soil water potential adjacent to the frog in the burrow was low enough for them to maintain water balance, then this would indicate that these frogs have the plasticity to switch between cocooning and non-cocooning strategies; such plasticity has not previously been appreciated, and this is an obvious area for further research.

The description provided by Slater & Main (1963) of the surface evidence that a frog has burrowed at a particular site (i.e. 'raised rim and loosely filled central crater') is similar to our observations for *N. nichollsi* and *N. aquilonius*. Our Aboriginal guides were very skilled at detecting frog burrows, even after approximately five to six months since they had been made. After noting the specific surface characteristics of burrows that were pointed out to us by our Aboriginal guides, we were able to locate burrows of *N. aquilonius* and *N. nichollsi* by ourselves.

The burrows of *N. nichollsi* and *U. micromeles* were often deeper than those of *N. aquilonius*, and consistent with the depth of *N. nichollsi* burrows reported by Slater & Main (1963) and Paltridge & Nano (2001). *Neobatrachus aquilonius* in the more compacted clay pan (site 3) had shallower burrows than those excavated in the swale (site 4). It is not known what influences the depth of the burrow dug by a frog. After heavy rain water would drain through the soil to lower levels and much would be lost by evaporation, so it would seem difficult for a frog to predict the water content (potential) for a particular depth months after a major rainfall event. Whether *N. aquilonius* dug deeper burrows in the swale because digging was easier than in the clay pan, or whether the depth was determined by some

environmental or physiological variable (e.g. energetic cost of burrowing) is unknown.

It is not known if *N. aquilonius* and *N. nichollsi* dig new burrows each time they become surface active or return to previously-used burrows. There is an obvious energy saving associated with burrowing into existing loosely-compacted burrows. However, relocating burrow openings at night might require frogs to have a 'mental' map of their activity area and the need to return to previously used burrows may limit the size of their activity area (i.e. there would be a high energy cost of returning to a burrow that is some distance away).

Water penetrates compacted clay soils slowly, compared with sandy or loosely compacted soils. It seems unlikely that rain would rapidly penetrate compacted clay soil to the depth of the frog, and stimulate it to escape from its cocoon, and dig its way to the surface so that it was surface active the first night after it rained. The shape of the burrow and the loose consistency of the soil in the burrow, compared to the greater compactness of the surrounding soil, provides an indication of how burrowed, cocoon-forming *N. aquilonius* are able to surface quickly after heavy rain. If a frog selects a burrowing site that is likely to have some run-on water, and pooling occurs on the surface even for a small time above the burrow opening, then water will percolate through the less compacted soil of the burrow down to the frog long before is penetrates down through the adjacent compacted soil to the same depth. In this way the frog's cocoon can become saturated, removed and eaten, and the frog surfaces and commences feeding, and perhaps even breeds, before water has soaked down through compacted soil to the depth at which it was burrowed. When a frog is ready to burrow again, it is likely that the surface water will have penetrated and softened the soil over a wider area and to a greater depth, making it much easier for the frog to burrow. Dimmitt & Ruibal (1980) reported that *Scaphiopus couchi* use low frequency sound or vibration as a cue for emerging from sandy soils. But it is difficult to imagine *N. aquilonius* removing and eating their cocoons, and digging their way to the surface in dry soil. Therefore, emergence stimuli for sand and clay burrowing frogs may be different because of the different rate that water percolates down through the soil profile.

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Temporal variations in reptile assemblages in the Goldfields of Western Australia

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Abstract

We report significant variation in reptile pit-trapping results for eleven survey periods over two and half years for nine sites in the Goldfields region of Western Australia. We collected a total of 51 species and 2868 individual reptiles from a surveying effort of 33264 pit-trap days. Year-to-year variation in relative abundances for particular species was greater than elsewhere reported as being the result of stochastic events such as fires. Seasonal variation in catch rates suggest that to adequately survey an area, pit-trapping programs need to be undertaken in more than one season. This has significant (financial) consequences for mining companies and other industries that employ consultants to undertake terrestrial fauna surveys to describe that component of the biodiversity for an area. Environmental protection agencies need to adjust their guidelines for terrestrial faunal surveys to adequately describe the biodiversity of an area. Our data indicate that before researchers can claim that year-to-year variation in reptile assemblages are due to stochastic events they must account for 'normal' year-to-year variations.

Keywords: reptile assemblage, fauna surveys, temporal variations, seasons, EIA, pit-trapping, Ora Banda

Introduction

Environmental consultants typically survey a site once and draw conclusions about the vertebrate faunal assemblage. For example, Fraser et al. (2003) having reviewed the adequacy of 15 terrestrial faunal surveys in the Goldfields region of Western Australia (WA) for the purposes of preparing an environmental impact assessment (EIA), reported that only three environmental consultants surveyed in two seasons, seven surveyed on one occasion and the remaining five did not explicitly indicate when they surveyed. EIAs are an important component in the planning and approval process for the development of a mine site or any other type of disturbance to the natural environment (Environmental Protection Authority 2002). Outcomes from terrestrial faunal surveys undertaken for purposes of preparing an EIA are the basis of decisions by government regulatory authorities on potential impacts of disturbance. Fauna survey data can also be used to monitor and judge the extent to which rehabilitation programs are able to recreate near-natural, self-sustaining, functional ecosystems at the conclusion of mining (Thompson 2004). Is it then reasonable for environmental consultants to survey an area in one season or even in a couple of seasons in a single year and presume to understand the vertebrate faunal assemblage for that area for purposes of preparing an EIA?

Some field ecologists have surveyed an area a couple of times and have drawn conclusions about the impact of stochastic events (e.g. rainfall, fire) on vertebrate assemblages, without reporting 'normal' seasonal and year-to-year variations for that assemblage. For example, James (1994) and Pianka (1996) have attributed changes in reptile assemblages to the impact of heavy rainfall or fires but have not been able to demonstrate the variations in relative abundance are greater than normal year-to-year variation due to local environmental and geophysical conditions that are within the normal range for that area. Cowan & How (2004) adequately demonstrated significant seasonal and long-term variation in small vertebrate assemblages in the eastern Goldfields and questioned the ability of short-term surveys to describe vertebrate assemblages for EIA.

The Goldfields region of WA has been extensively mined for over a century and terrestrial fauna surveys undertaken for purposes of preparing EIA's are a relatively common occurrence in this region. Reptile assemblages in this and other mining areas of WA are generally estimated based on trapping (pit-traps and Elliott traps) and hand searching programs (Fraser et al. 2003). Before we can make judgements about the impact of stochastic events (e.g. fire, rainfall) on reptile assemblages in arid and semi-arid Australia, it is important to understand natural seasonal and year-to-year variations, the impact of heavy rainfall events and fires, and the sessional processes after these stochastic events. Our objective is to report variations in reptile assemblages from season-to-season, and year-to-year when the survey effort remained constant for a semi-arid, Eucalypt-Casuarina-Mulga woodland in the Goldfields region of WA in the context of detailed
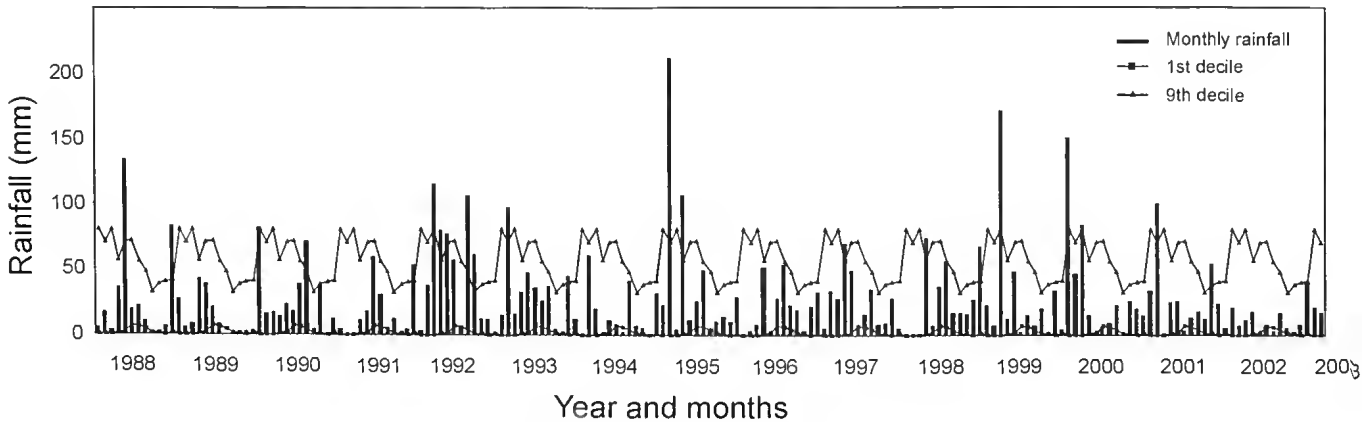
Figure 1. Cumulative monthly rainfall at Placer Dome Asia Pacific, Kalgoorlie West Operations from 1988 until 2003.

information on local rainfall, a reported major determinant of reptile abundance (Bradshaw *et al.* 1991; James 1991, 1994; Saint Girons *et al.* 1992; Spiller & Schoener 1995; Dickman *et al.* 1999).

'Normal' in the context of rainfall is difficult to define in the goldfields region. Variability is demonstrated by the histogram (Fig 1) of cumulative monthly rainfall for Placer Dome Asia Pacific, Kalgoorlie West Operations (the closest weather station to our study sites) showing the 1st and 9th deciles for rainfall at the Kalgoorlie-Boulder Airport (calculated from 1939 to 2001), which is about 50km to the south.

Methods

Study sites

We have used data collected over a two and a half year period for nine relatively undisturbed sites (Gimlet, Palace, Rose, Wendy Gully, Salmon Gums, Spinifex, Davyhurst, Security and Crossroads) in the gold mining region of Ora Banda (30° 27' S, 121° 4' E; approximately 50 km north of Kalgoorlie; Fig 2), WA. Ora Banda lies on Archaen granites that underlie lateritic gravel soils. The vegetation was heterogenous, ranging from Eucalypt-Casuarina-Mulga woodlands interspersed with *Acacia*, to sparsely distributed spinifex (*Triodia* spp.) and shrubs (*Acacia* spp.) to dense shrubs (*Acacia* spp., *Atriplex* spp., *Allocasuarina* spp.). Each of the nine sites was chosen because they represented a different vegetation type but were typical for the area (Mattiske Consulting Pty Ltd 1995). There was no indication of fires in the records of the mining companies that had control over the tenements on which the study sites were located or fire scars on the vegetation to suggest any of the sites had been recently burnt. Because of the sparseness of the vegetation and lack of undergrowth major fires in this area are rare, but when they occur they are generally remembered by people that live and work in the area.

Weather information

Minimum and maximum ambient temperature, and cloud cover data, for each survey period were collected from the Bureau of Meteorology in Kalgoorlie (http://www.bom.gov.au/climate/ averages/tables/cw_012038.shtml), the closest government weather station. Rainfall data came from Placer Dome Asia Pacific, Kalgoorlie West Operations, which was within 25 km of all study sites. Rainfall, particularly summer thunderstorms, can be localised and the mine site data better represents rainfall at our sites than that from the Bureau of Meteorology in Kalgoorlie, which is further away. The Kalgoorlie Bureau of Meteorology has kept records for the Kalgoorlie-Boulder site since 1939 and Placer Dome Asia Pacific, Kalgoorlie West Operations has kept records since 1988. Means and percentiles were calculated for these periods.

Data collection strategies

All sites were pit-trapped on eleven occasions between September 2000 and January 2003 (September and December in 2000; January, April, June, September and December in 2001; January, April and June in 2002; and January 2003) using alternating 20 L PVC buckets and 150 mm PVC pipes (600 mm deep) joined by 250 mm high x 30 m long fly-wire drift fences. Each site had eight rows of six pit-traps (Fig 2). All pit-traps were dug in during June-July 2000 to minimise potential digging-in effects on reptile capture rates. During each surveying period, each pit-trap was opened for seven days and pit-traps were cleared daily. In September, December and January survey periods, pit-traps were divided into two groups and surveyed in successive weeks. Mean minimum and maximum ambient temperatures for these two seven day periods were not significantly different for all survey periods, so weather data were combined for these periods and means are reported for each surveying period. Each reptile captured was sexed (where possible), weighed and measured. Most reptiles were identified before immediately being released adjacent to its point of capture; a few were vouchered with the Western Australian Museum (WAM). Recaptures have been included in the analysis. We report 33264 pit-trap days of data.

We appreciate that there was approximately three months gap between the September-December, January-April, April-June and June-September surveying periods and a much shorter period between December-January surveying. As a consequence, it is probable that the December and January catches would be more similar than the other surveying periods because they are closer together. Most reptile surveys are undertaken in the

Layout of pit-traps in undisturbed areas
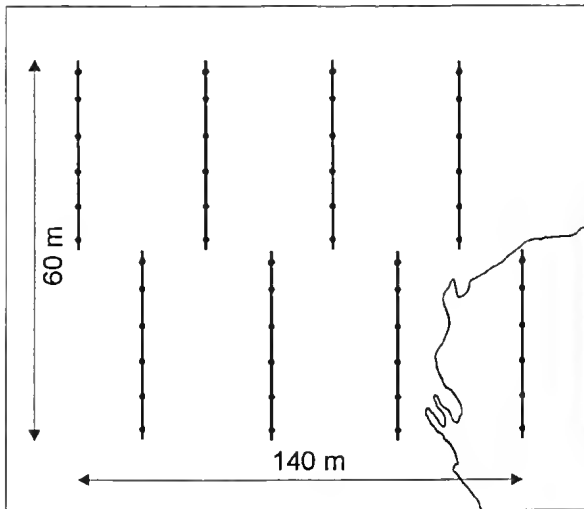
Study sites around Ora Banda
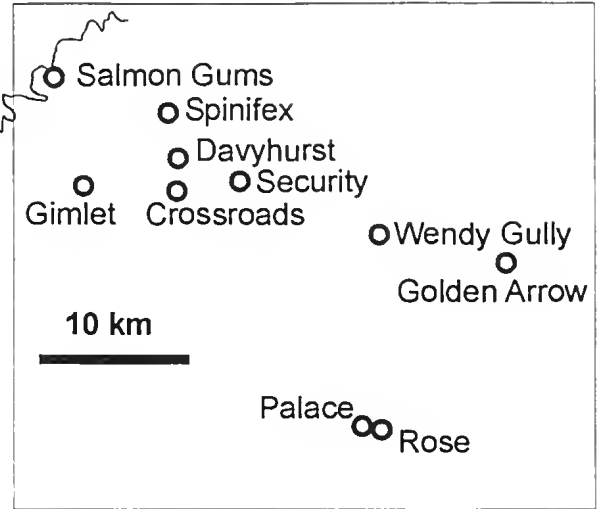
Figure 2. Location of Ora Banda, nine study sites and pit-trap layout.

warmer months, but there is limited commentary in the literature on whether there are differences in the composition of pit-trapping catches within this period (however, see Cowan & How 2004). We chose to survey in both December and January to assess the similarity of catches within this period.

Data analysis

We examined reptile assemblage structure for the Ora Banda region by combining seven days of pit-trap data for each of the nine sites and then compared reptile assemblages for each of the eleven surveying periods (3024 pit-trap days for each period).

We report the total number of species caught in the surveying period, diversity using log-series (a), Shannon's (H) and Simpson's (D) diversity indices (using Pisces Conservation Ltd 2002, Species Diversity and Richness II software). Log-series diversity has good discriminating ability, low sensitivity to sample size and is widely used (Magurran 1988). Shannon's and

Simpson's diversity indices are included as they are commonly reported and these data can be compared with other reports. We measured and report evenness (J; using Pisces Conservation Ltd 2002, Species Diversity and Richness II software) and similarity using Morisita-Horn index (using Colwell 1997, EstimateS software). Tramer's (1969) measure of evenness is widely used and the Morisita-Horn similarity index was used because it accounts for relative abundance and was recommended by Magurran (1988).

Results

Weather for the survey period

Typically, the Goldfields region of WA has hot summers and cool winters (Table 1). Rainfall episodes in winter are generally less than 20 mm and more frequent, whereas summers are characterised by many days of no rainfall and a few days of unpredictable rainfall mostly

Table 1

Rainfall (mm) and temperature (°C) statistics for Kalgoorlie-Boulder airport from 1939 to 2004

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Mean monthly rainfall	22.8	31.5	23.6	22.1	27.8	29.6	25.4	21.7	14.5	15.1	18.2	16.1
1st decile of monthly rainfall	0.3	0	0.4	1	2.4	6.2	5.5	4.5	0.7	0.9	0.4	1.3
Median monthly rainfall	7.1	12.5	9	14.8	21.8	21	20.8	15.9	11.2	9.4	15.3	11
9th decile of monthly rainfall	74	74.2	80.1	56.5	67.9	68.2	53.1	46.7	31.4	36.4	40.4	41.4
Lowest monthly rainfall	0	0	0	0	0	2.1	0.6	1.6	0.3	0	0	0
Highest monthly rainfall	185.9	307.8	197.0	98.6	110.2	185.7	82.6	74.0	98.3	84.4	115.4	88.6
Highest recorded daily rainfall	154.4	177.8	70	49.8	45.2	57.2	28.6	49.6	44.2	45.6	77	28.2
Mean daily maximum temperature	33.6	32	29.5	25.1	20.5	17.5	16.7	18.4	22.2	25.6	28.9	31.9
Mean daily minimum temperature	18.2	17.8	16.0	12.6	8.6	6.2	4.9	5.5	7.9	10.9	14.0	16.5

Table 2

Total number of individuals caught, total number of species caught, number and percentage of hatchlings caught for each family, diversity and evenness values for the combined nine sites around Ora Banda for each of the eleven survey periods

	Sep-00	Dec-00	Jan-01	Apr-01	Jun-01	Sep-01	Dec-01	Jan-02	Apr-02	Jun-02	Jan-03	Change Sep	Change Dec	Change Jan	Change Apr	Change Jun	Change Jan 01 to 02, 03
Agamids																	
Caimanops amphiboluroides	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0, 1
Ctenophorus cristatus	0	0	4	0	0	0	0	2	0	0	0	0	0	-2	0	0	-2, -4
Ctenophorus reticulatus	9	2	14	0	1	7	1	12	1	0	4	-2	-1	-2	1	-1	-2, -10
Ctenophorus scutulatus	3	0	3	0	1	3	1	2	2	0	0	0	1	-1	2	-1	-1, -3
Moloch horridus	5	1	2	0	0	1	3	1	8	0	0	-4	2	-1	8	0	-1, -2
Pogona minor	10	5	12	2	0	8	4	5	3	0	7	-2	-1	-7	1	0	-7, -5
Tympanocryptis cephala	5	2	0	0	0	0	0	0	0	0	0	-5	-2	0	0	0	0, 0
Geckos																	
Diplodactylus granariensis	77	44	45	9	1	37	40	47	18	1	27	-40	-4	2	9	0	2, -18
Diplodactylus maini	61	47	49	36	0	42	46	48	20	0	52	-19	-1	-1	-16	0	-1, 3
Diplodactylus pulcher	38	64	79	28	0	32	28	63	26	0	74	-6	-36	-16	-2	0	-16, -5
Gehyra purpurascens	0	4	12	1	0	0	1	1	0	0	0	0	-3	-11	-1	0	-11, -12
Gehyra variegata	12	22	65	9	1	4	14	23	7	0	9	-8	-8	-42	-2	-1	-42, -56
Heteronotia binoei	1	11	15	4	0	2	5	3	2	0	21	1	-6	-12	-2	0	-12, 6
Oedura reticulata	0	0	4	0	0	0	0	0	0	0	1	0	0	-4	0	0	-4, -3
Rhynchoedura ornata	1	21	30	16	0	8	7	7	4	0	30	7	-14	-23	-12	0	-23, 0
Strophurus assimilis	25	43	24	0	0	12	12	20	1	0	4	-13	-31	-4	1	0	-4, -20
Underwoodisaurus milii	6	11	11	4	0	4	3	12	6	0	5	-2	-8	1	2	0	1, -6
Pygopods																	
Delma australis	3	6	3	2	0	0	0	5	0	0	1	-3	-6	2	-2	0	2, -2
Delma butleri	0	1	0	0	0	0	0	2	0	0	0	0	-1	2	0	0	2, 0
Delma fraseri	0	1	1	0	0	0	0	0	0	0	0	0	-1	-1	0	0	-1, -1
Lialis burtonis	2	0	0	0	0	1	0	0	0	0	0	-1	0	0	0	0	0, 0
Pygopus lepidopodus	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	0	0, -1
Skinks																	
Cryptoblepharus plagiocephalus	4	10	5	0	1	4	2	2	1	0	1	0	-8	-3	0	-1	-3, -4
Ctenotus atlas	13	10	23	3	0	4	4	9	1	0	3	-9	-6	-14	-2	0	-14, -20
Ctenotus schomburgkii	0	0	0	1	0	0	0	0	0	0	0	0	0	0	-1	0	0, 0
Ctenotus uber	19	17	19	5	0	8	3	17	14	0	5	-11	-14	-2	9	0	-2, -14
Cyclodomorphus m. elongatus	8	7	8	0	0	3	0	5	1	0	2	-5	-7	-3	1	0	-3, -6
Egernia depressa	19	21	29	4	0	1	1	4	3	0	8	-18	-20	-25	-1	0	-25, -21
Egernia formosa	0	4	5	0	0	1	0	1	0	0	1	1	-4	-4	0	0	-4, -4
Egernia inornata	1	1	14	4	0	1	5	14	0	0	7	0	4	0	-4	0	0, -7
Egernia striata	0	0	0	0	0	3	2	4	0	0	3	3	2	4	0	0	4, 3
Eremiascincus richardsonii	0	0	2	3	0	0	3	4	0	0	2	0	3	2	-3	0	2, 0
Hemiergis i. initialis	3	2	2	0	0	4	3	0	0	0	0	1	1	-2	0	0	-2, -2
Lerista muelleri	1	17	9	0	0	0	7	8	1	0	5	-1	-10	-1	1	0	-1, -4
Lerista picturata	4	31	21	2	0	6	6	12	4	0	8	2	-25	-9	2	0	-9, -13
Menetia greyii	37	8	12	15	0	2	6	3	5	0	1	-35	-2	-9	-10	0	-9, -11
Morethia butleri	8	9	4	2	0	0	6	1	3	0	4	-8	-3	-3	1	0	-3, 0
Tiliqua occipitalis	1	0	0	0	0	0	0	1	1	0	0	-1	0	1	1	0	1, 0
Tiliqua rugosa	0	1	0	0	0	2	1	0	0	0	0	2	0	0	0	0	0, 0

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Varanids																	
Varanus caudolineatus	1	8	9	3	0	3	1	5	1	0	3	2	-7	-4	-2	-4	-6
Varanus gouldii	0	4	4	0	0	0	1	2	2	0	1	0	0	1	0	1	0
Varanus tristis	0	0	0	0	0	0	0	1	0	0	0	0	-3	-2	2	-2	-3
Blind snakes																	
Ramphotyphlops australis	12	1	6	0	0	1	3	6	0	0	10	0	0	0	0	0	0
Ramphotyphlops bituberculatus	1	1	1	0	0	0	0	0	0	0	0	7	2	0	0	0	4
Ramphotyphlops hamatus	6	7	11	1	0	13	0	18	1	0	3	-1	-7	7	0	7	-8
Elapids																	
Brachyurophis semifasciata	0	9	4	0	0	0	0	4	0	3	0	0	0	0	0	0	0
Demansia psammophis	0	0	0	0	0	1	1	0	0	1	0	0	-9	0	0	0	-1
Parasuta monachus	4	6	2	0	0	4	6	6	3	1	1	-1	1	4	3	4	-1
Pseudonaja modesta	1	1	1	0	0	0	0	0	0	0	0	-1	-1	-1	0	-1	-1
Simoselaps bertholdii	0	2	2	0	0	3	0	1	0	1	0	0	1	-1	0	-1	-1
Suta fasciata	1	0	1	0	0	2	1	1	0	1	1	-1	2	0	0	0	0
# of Agamidae	32	10	35	2	2	19	9	22	14	0	12	-13	-1	-13	12	-13	-23
# of Gekkonidae	221	267	334	107	2	141	156	224	84	1	223	-80	-111	-110	-23	-110	-111
# of Pygopodidae	5	8	5	2	0	2	0	8	0	0	1	-3	-8	3	-2	3	4
# of Scincidae	118	140	151	39	1	39	43	85	33	0	50	-79	-97	-66	-6	-66	-101
# of Varanidae	1	12	13	3	0	3	2	8	3	0	4	2	-10	-5	0	-5	-9
# of Typhlopidae	19	9	18	1	0	14	3	24	1	0	13	-5	-6	6	0	6	-5
# of Elapidae	6	18	10	0	0	3	10	12	3	1	7	-3	-8	2	1	6	-3
Total # of individuals caught	402	464	566	154	5	221	223	383	138	2	310						
Total # of species caught	34	39	40	21	5	30	32	40	25	2	35						
# of hatchling agamids (%)	*	*	16 (45.7)	*	*	*	*	7 (31.8)	3 (21.4)	*	*						
# of hatchling geckos (%)	*	4 (1.5)	16 (4.8)	*	*	*	1 (0.6)	3 (1.3)	3 (3.6)	*	3 (1.3)						
# of hatchling pygopods (%)	*	*	2 (40.0)	*	*	*	*	*	*	*	*						
# of hatchling skinks (%)	5 (4.2)	8 (5.7)	9 (6.0)	7 (17.9)	*	1 (2.6)	2 (4.7)	5 (5.9)	8 (24.2)	*	3 (6.0)						
# of hatchling varanids (%)	*	*	4 (30.8)	2 (66.7)	*	*	*	*	1 (33.3)	*	*						
# of hatchling blind snakes (%)	1 (16.7)	*	1 (5.6)	*	*	1 (33.3)	*	*	*	*	1 (7.7)						
# of hatchling elapids (%)	*	*	*	*	*	*	*	*	*	1 (100.0)	*						
# of hatchling in total sample (%)	6 (1.5)	12 (2.6)	48 (8.5)	12 (7.8)	*	4 (1.8)	1 (0.5)	15 (3.9)	15 (10.9)	1 (50.0)	7 (2.3)						
Simpson's diversity index	11.21	15.87	16.24	8.71	⊗	10.41	9.97	13.62	10.99	⊗	9.09						
Shannon's diversity index	2.80	3.07	3.11	2.49	⊗	2.74	2.75	3.01	2.67	⊗	2.70						
Log series diversity	8.87	10.16	9.84	6.57	⊗	9.36	10.23	11.24	8.92	⊗	10.13						
Evenness	0.70	0.77	0.78	0.62	⊗	0.69	0.69	0.75	0.67	⊗	0.68						
Mean minimum temperature (°C)	10.4 ± 0.91	15.6 ± 0.69	23.1 ± 0.70	12.3 ± 1.39	4.1 ± 0.76	10.6 ± 1.15	12.6 ± 0.51	17.3 ± 0.74	14.6 ± 0.59	5.8 ± 0.58	18.1 ± 1.00						
Mean maximum temperature (°C)	26.6 ± 1.04	31.5 ± 1.55	38.5 ± 0.86	25.7 ± 1.77	21.6 ± 0.84	26.1 ± 1.43	24.8 ± 0.98	32.0 ± 1.19	27.3 ± 0.88	19.9 ± 0.50	31.0 ± 1.83						
Mean rainfall (mm)	0	0.4 ± 0.28	0	0	0	0.4 ± 0.39	0.3 ± 0.00	0.9 ± 0.85	0.1 ± 0.00	0	1.9 ± 1.20						
Mean cloud cover (oktas)	2.5 ± 0.60	2.4 ± 0.61	4.3 ± 0.52	4.2 ± 1.00	1.3 ± 0.67	3.8 ± 0.73	5.2 ± 0.58	3.5 ± 0.55	3.3 ± 0.72	1.8 ± 0.50	3.9 ± 0.79						

⊗ species and abundances are too low to estimate values, # = number, for weather variables means ± 1 se are shown

* no hatchlings were caught during this survey period, numbers in parentheses indicate percentage of hatchlings caught during that survey period for that taxonomic group
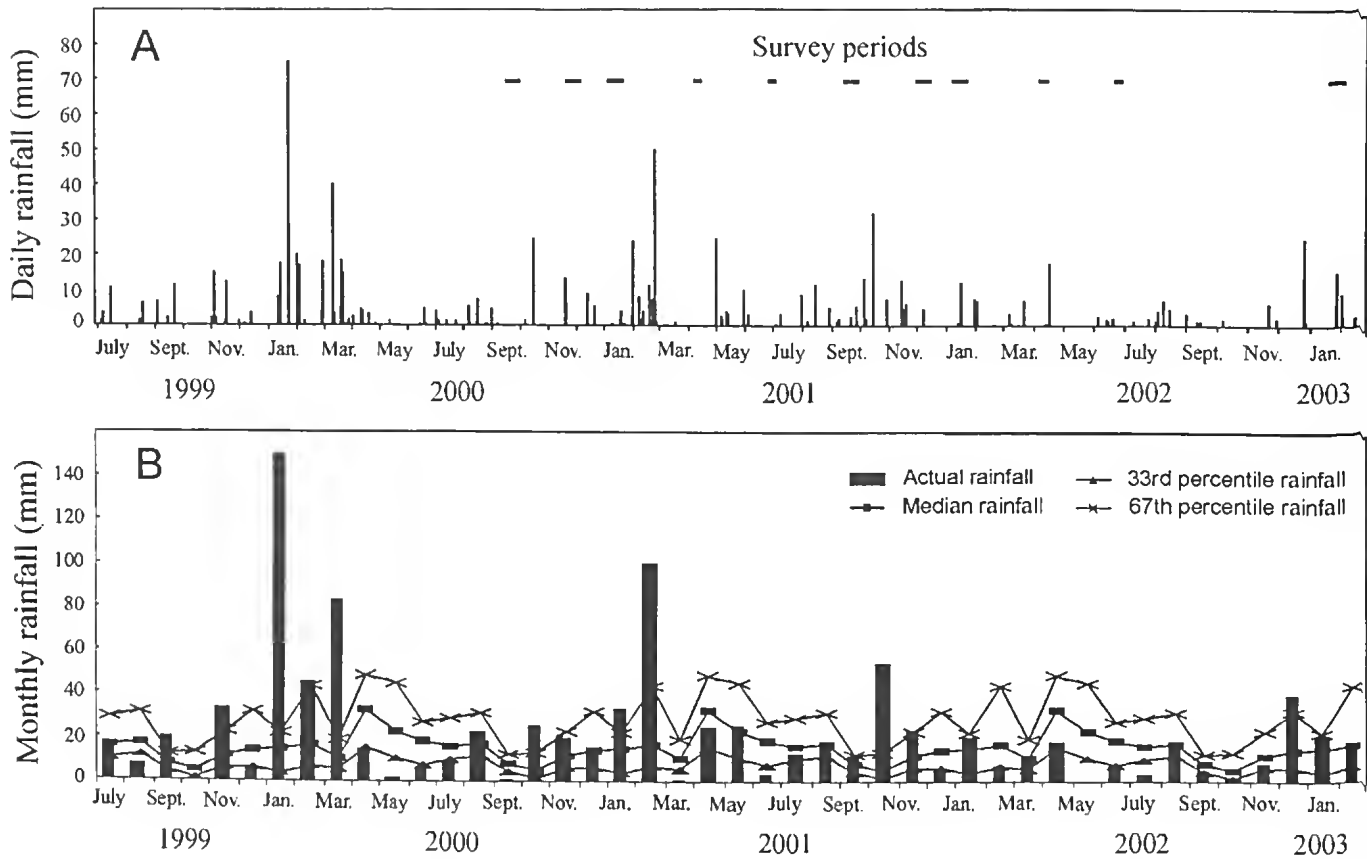
Figure 3. Daily rainfall from July 1999 until February 2003 taken at Placer Dome Asia Pacific, Kalgoorlie West Operations with days in which pit-traps were open indicated (horizontal bars; A) and monthly rainfall, median rainfall, 33rd and 67th percentiles (B) based on data taken from the Bureau of Meteorology in Kalgoorlie from 1939 to 2001.

from thunderstorms or decaying tropical depressions that can precipitate large quantities of rain over a couple of days (Fig 3A). Two decaying tropical depressions produced a significant amount of rain in January (103 mm) and March (40 mm) 2000, and a heavy localised thunderstorm in February 2001 produced 63 mm of rainfall (Fig 3A; n.b. rainfall for 2 successive days have been added to obtain these totals). Total rainfall for January to March in 2000 was 278 mm, for January to March in 2001 it was 134 mm, and for January to March in 2002 it was 38 mm. Summer rainfall greater than 40 mm in a 24 hour period was apparent in 1988, 1992, 1993, 1994, 1995, 1999, 2000 and 2001.

Heavy rains in January and March 2000 (Fig 3A) resulting from decaying tropical depressions caused some of the annuals to sprout and flower, and some of the perennials to flower in the months that follow (pers. obs.). There was one day in October 2000 where 24.5 mm of rain was recorded and this took the monthly average above the 67th percentile (Fig 3B). This rain fell between the September and December 2000 survey periods. Heavy rain recorded in January and February 2001 was between the January and April 2001 survey periods. There was 0.75 mm of rain in March and no rain until 19 April 2001. Because there was no 'follow-up' rains most of the annuals that sprouted died and the heavy January/ February rains did not translate into substantial vegetation regrowth. Similarly, the 32 mm of rain on 14 October 2001 had 7 mm of 'follow-up' rain on 29 October

and another 12 mm on 15 November. These follow-up rains were insufficient to sustain most of the annuals that sprouted after the 14 October rains. Thirty nine mm of rain over three days (25–27) in December 2002 had follow-up rains of 21 mm on 27–28 January 2003.

Mean minimum and maximum ambient daily temperature and cloud cover are reported for the Kalgoorlie-Boulder Airport and rainfall for Kalgoorlie West Operations in Table 2 for each survey period. Mean minimum and maximum daily temperatures in December and January of 2000/01 were significantly higher (t_{26} =3.40, $P < 0.001$ min. t_{26} = 3.66, $P < 0.01$ max. Dec.; t_{26} = 5.65 $P < 0.001$ min, t_{26} = 4.43, $P < 0.001$, max. Jan.) than for the same survey periods in 2001/02. Mean minimum or maximum ambient daily temperatures for September 2000 or April of 2001 did not differ significantly from those in the same periods in the subsequent years.

Reptiles

We caught 2868 individuals from 51 reptile species across nine sites during eleven survey periods (Table 2). Catch numbers and measured species richness were appreciably lower in June for both years (2001, 5 and 2002, 2). Measured species richness and the total number of individuals caught were highest of all survey periods in January for both 2001 (566 individuals, 40 species) and 2002 (383 individuals and 40 species; Table 2). Spring (September) surveying yielded a significantly higher

Table 3

Similarity (Morisita-Horn similarity index) among survey periods (excluding June)

	Sep-00	Dec-00	Jan-01	Apr-01	Sep-01	Dec-01	Jan-02	Apr-02
Dec-00	0.81							
Jan-01	0.75	0.91						
Apr-01	0.75	0.75	0.77					
Sep-01	0.92	0.83	0.78	0.83				
Dec-01	0.91	0.84	0.80	0.84	0.95			
Jan-02	0.85	0.92	0.91	0.80	0.92	0.90		
Apr-02	0.84	0.84	0.83	0.84	0.89	0.87	0.91	
Jan-03	0.71	0.82	0.82	0.90	0.85	0.84	0.87	0.87

number of individuals and species than autumn (April) for both years (402 vs 154 individuals, 34 vs 21 species in 2000/01, 221 vs 138 individuals, 30 vs 25 species in 2001/02). More reptiles were caught in the first 12 months of surveying than in the second 12 months (September to April 2000/01 1591 vs 967 in 2001/02).

As might be expected, various measures of species diversity were highest when catch rates and species richness were highest (Table 2). Similarity scores greater than 0.9 demonstrated high similarity in species richness and abundance for January 2002 with December 2000 (0.92) and 2001 (0.90), January 2001 (0.91) and September 2001 (0.92; Table 3). Noticeably lower similarity scores (i.e. < 0.80) were recorded for April 2001 with September 2000 (0.75), December 2000 (0.75) and January 2001 (0.77); catches in September 2001 were comparatively dissimilar to January 2001 (0.78); and September 2000 differed appreciably from January 2003 (0.71).

We caught seven species of agamids. The two most abundant were *Pogona minor* (56 captures) and *Ctenophorus reticulatus* (50 captures) and these were mostly caught in September and January surveying periods (Table 2). Gravid *P. minor* were often seen on gravel roads around Ora Banda during September in both surveying years. Increased capture rates for these two species in January reflected the number of hatchlings caught. Although the numbers of other agamids (*Ctenophorus scutulatus*, *Tympanocryptis cephala*, *Ctenophorus cristatus* and *Caimanops amphiboluroides*) caught were low, the catch pattern was similar to that for *P. minor* and *C. reticulatus*, except for *Moloch horridus*. *Moloch horridus* captures did not appear to conform to any particular pattern of activity other than they were not caught in June (Table 2).

We caught 10 species of geckos. The most abundant geckos were *Diplodactylus granariensis* (346), *D. maini* (401) and *D. pulcher* (432). The abundance pattern for geckos appeared to be closely linked with ambient temperature. Catch rates for January (334 for 2001 and 224 for 2002) were higher than for December (267 for 2000 and 156 for 2001), which in turn were higher than for September (221 for 2000 and 141 for 2001) for both years. The number of geckos caught in April (107 for 2001 and 84 for 2002) was less than that caught in September, December and January.

Seventeen species of skinks were caught. Two of these belong to the genus *Tiliqua*, which because of their size, were not often caught in pit-traps but were occasionally seen on gravel roads, particularly in September. Of the smaller and more easily pit-trapped skink species, the most abundant were the terrestrial foraging *Ctenotus uber* (107) and *C. atlas* (70), arboreal *Egernia depressa* (90), fossorial *Lerista picturata* (89) and the very small terrestrial litter dwelling *Menetia greyii* (93). The pattern of captures for small skinks was similar to that for geckos, with January (151 in 2001 and 85 in 2002) captures being higher than for December (140 in 2000 and 43 in 2001), which in turn was higher than for September (118 in 2000 and 39 in 2001), which was higher than for April (39 in 2001 and 33 in 2002). The number of skinks caught in the second summer (200) was appreciably less than caught during the same period in 2000/01 (448). The skink species most noticeably different to this pattern was *Menetia greyii*. More than a third (37/93) of all captures for *M. greyii* were caught in September 2000, the next highest number of individuals caught was April 2001 (15), followed by January 2001 (12) and December 2000 (8; Table 2). For the second summer, catch rates for this species were low for each of the four surveying periods in the warmer months (Table 2).

We caught three species of blind snakes; *Ramphotyphlops australis* (39), *R. hamatus* (60) and *R. bituberculatus* (3). Catch rates for the two most abundant species provided a consistent pattern across the two years, with comparatively higher numbers being caught in September and January and lower numbers in December and less in April (Table 2). More *R. australis* than *R. hamatus* were caught in September 2000 (12 vs 6), December 2001 (3 vs 0) and January 2003 (10 vs 3), but the reverse was the case for the other survey periods.

The number of elapids, varanids and pygopods caught was low and trends were difficult to detect (Table 2).

Hatchlings

Hatchlings were most frequently pit-trapped in January and April. For summer 2000/01, the proportion (number of hatchlings for each taxonomic group / total number of individuals for each taxonomic group) of hatchlings caught in January (8.5%) and April (7.8%) was similar, although more hatchlings were caught in January (48) than April (12; Table 2). However, in the summer of 2001/02 there was a higher proportion of hatchlings caught in April (10.9%) than January (3.9%), and the overall number of hatchlings caught in January 2002 (15) was less than in 2001 (48). Hatchling agamids were plentiful in January 2001 (16), less abundant in January 2002 (7) and none were caught in January 2003

(Table 2). Hatchling geckos were most abundant during January 2001 (16) with low numbers being caught during the other two January survey periods (3 in both 2002 and 2003). Hatchling skinks were caught in similar numbers for December (8), January (9) and April (7) 2000/01 survey periods, but were only caught in similar numbers again in April 2002 (8: Table 2).

Discussion

Variation on weather patterns

During our two and half year survey (September 2000 – January 2003), summer rains (with the necessary follow-up rains) that resulted in many of the annuals growing to maturity and flowering, and the perennials flowering only occurred after the heavy rains in January 2000. The effect of these rains on reptile abundance in the following spring and summer are unknown and difficult to quantify without data for the same period in previous years. Heavy summer rain may damage reptile eggs buried in the ground reducing recruitment, as many of the hatchlings were first detected in January. These rains may have increased survivorship of those individuals that hatched because of the additional food supply (Haynes 1996). The number of reptiles caught in the spring-summer of 2000/01 was greater than for the following spring-summer, which may have been a consequence of the heavy January 2000 rainfall. There were three other significant rainfall events (February 2001, October 2001 and December 2003) within the two and one half year survey period that potentially could have affected reptile abundance. Heavy rainfall in February and October 2001 had insufficient 'follow-up' rain to result in an appreciable change in the vegetation and therefore prey abundance (Dunham 1978; Dickman *et al.* 1999). The December 2002 rainfall was too close to our survey period in January 2003 to have an affect on the number of individuals caught.

Potential impact of rainfall on reptile abundance

Terrestrial reptile reproductive output (clutch size, number of clutches and survivorship) and growth are influenced by preceding rainfall for many arid and semi-arid reptiles (Nagy 1973; Bradshaw *et al.* 1991; James 1991; Castilla *et al.* 1992; Saint Girons *et al.* 1992; Tinkle *et al.* 1993; Spiller & Schoener 1995; Dickman *et al.* 1999), although Whitford & Creusere (1977) reported that there was no correlation between summer rainfall (June-July) and changes in reptile density in the Chihuahuan Desert. If heavy rainfall was to have an affect, then when rainfall exceeded the 67th percentile it should be followed by some change in relative catch abundance of reptiles. Rainfall exceeded the 67th percentile for the months of January, February and March 2000 and the effects should have been evident in the following autumn and perhaps the subsequent spring surveys. Heavy rains were again recorded in January and February 2001, which should have affected reptile abundance in the following autumn, and the spring survey, if the affect carried over the winter months. If rainfall generally increased reptile abundance, then the above 67th percentile rains that were recorded in October 2001 should have recorded an affect for the surveys during December 2001, and January and April 2002, and above the higher than 67th percentile

rains in December 2002 may have had an affect on reptile abundances for the January 2003 survey (if it was not too soon). There is insufficient chronosequenced captures to examine species-specific data statistically, but an examination of overall catch rates shows no systematic changes in reptile numbers overall, or for any of the families (Table 2), following these above the 67th percentile months of rainfall. The overall pattern of change between years and seasons, therefore does not appear to have been noticeably affected by heavy rainfall events. However, as pointed out by Dickman *et al.* (1999), it is possible for one species in a family to increase in abundance and a sister species to decrease in abundance in response to rain and for one affect to mask the other.

Seasonal variation

Ectothermic reptiles were not expected to be active during the month of June around Ora Banda, and pit-trap captures reflected daily ambient temperatures that were too low to enable most reptile species to be surface active, and thus caught in pit-traps. Obviously, terrestrial fauna surveys undertaken during the cooler months are unlikely to provide an adequate indication of herpetofauna in the area. Although this seems obvious, environmental consultants continue to undertake terrestrial fauna surveys in the cooler months for the purposes of recording the fauna (including reptiles) in areas that are likely to be disturbed by a potential development. Inappropriate or a lack of guidance from the appropriate government environmental protection authorities may, in part, be responsible for this.

We recorded 51 pit-trappable species of reptiles in the Ora Banda area, however, the highest number of species caught during the 3024 pit-trapping days for any of the eleven survey periods was only 40 species during January 2001 and 2002. Similarity scores indicated that active, and available to be caught reptile assemblages, varied significantly among seasons (Table 3). Taken together, these two results suggested that our trapping effort during each survey was insufficient to catch all the species that could be caught in the area during any survey period (also see Thompson *et al.* 2003) and that pit-trapping must be undertaken in more than one season to obtain an accurate appreciation of the reptile assemblage in the Goldfields region of WA, a view expressed by Fraser *et al.* (2003) and Cowan & How (2004). The EPA (2004) indicated that surveys conducted for baseline information (i.e. the first survey of the area prior to development) should be undertaken in multiple seasons (pp. 12), however, few EIAs are based on multiple surveys as suggested by this guidance statement. Our data indicate that pit-trapping fauna surveys in January provided the highest number of individual captures (individuals per 10 pit-trap nights: September 1.33 and 0.73, December 1.53 and 0.74, January 1.87, 1.27 and 1.03, and April 0.51 and 0.46) and highest measured species richness (September 34 and 30, December 39 and 32, January 40, 40 and 35, and April 21 and 25). Similarity scores for January and September (0.75, 0.85, 0.71, 0.78, 0.92, 0.85) or January and April (0.77, 0.83, 0.80, 0.90, 0.91, 0.87) were often less than 0.90, indicating that the species caught and their relative abundance varied between these two survey periods. Similarity scores between January and December (0.91, 0.92, 0.82, 0.80, 0.90, 0.84) were generally the highest

(Table 3), as might be expected due to the closeness of these two survey periods and the similarity in weather conditions. January data include more hatchlings than the December data and for some species only hatchlings were caught (e.g. *Ctenophorus cristatus*). Some of the larger varanids (e.g. *Varanus gouldii*) and adult large agamid lizards (e.g. *Ctenophorus cristatus*) are difficult to pit-trap in either 20 L PVC buckets or 150 mm PVC pipes (600 mm deep) as they can easily jump over 150 mm diameter pipes and jump out of 20 L buckets. More individuals were caught in spring than in autumn, increasing the probability of more species being caught in spring. As the difference in similarity scores is slightly greater between January and September, than January and April, these data suggested that where two surveys are to be undertaken they should occur in September and January to provide a better appreciation of the reptile assemblage. These findings are different to those of How (1998) who reported that a fauna survey in November and December on the mesic Swan Coastal plain of WA yielded appreciably higher catches (4.35 and 5.03 individuals per 10 pit-trap nights respectively) than either spring (1.36 for September and 1.32 for October), autumn (April 1.72), January (2.68) or February (1.78).

James (1994) suggested that it was difficult to disentangle reptile assemblage responses to seasonal changes in temperature from responses to changes in rainfall. James (1994) compared variation in lizard assemblages in each spring and autumn over a two year period (spring 1985 to spring 1987) for a 50 ha spinifex grassland on a dune-swale system south of Alice Springs in central Australia. He reported little rainfall in the first season, however, the second season (November 1986–March 1987) was affected by unusually heavy winter (June and July) rains, and the third season was dry. He concluded that the changes in hydric conditions profoundly influenced lizard population dynamics and reproductive activity, although he was unable to factor out 'natural' year-to-year variation in lizard assemblages for the area when conditions were within the 'normal' range. Similar to our results, James (1994) reported some species were more abundant in spring than autumn (e.g. *Ctenophorus isolepis, Diplodactylus conspicillatus*), while other species were more abundant during autumn than spring (e.g. *Rhynchoedura ornata*). Masters (1996) reported significant seasonal variation in both total abundance and number of reptile species caught during her surveys (sites burnt in 1976) of spinifex dominated sandplains with scattered shrubs west of Ayers Rock. May and August surveys generally had lower numbers of both individuals and species, similar to our results for cooler conditions.

Our data indicate that if resources are available, a comprehensive terrestrial fauna surveys (150 individuals caught using a combination of 20 L PVC buckets, 150 mm PVC pipes and funnels traps joined by drift-fences for each habitat type; authors unpub. data) should be undertaken in late spring (September – October), January and autumn (March–April) to provide the best understanding of reptile assemblages in the goldfields. If resources are limited, our data indicate the surveying effort is best applied in two periods; late spring (September–October) and January, rather than spreading the surveying effort (and resources) over three periods. Inadequate survey effort to assess species richness for the

purpose of preparing an EIA is a serious problem in Australia (Benkendorff 1999). Thompson *et al.* (2003) provide a commentary on this issue and explained how species accumulation curves can be used to estimate the pit-trapping effort necessary to capture a nominated proportion of the species in an area. Cowan & How (2004) pointed out that there are appreciable variations in capture rates for reptiles between Spring and Autumn surveys and suggested one-off short-term surveys are inadequate to determine vertebrate assemblages for EIA purposes, a view we would strongly support.

Year-to-year

Year-to-year variations in reptile assemblages were appreciable between the two years surveyed (see similarity scores in Table 3). Read (1992, 2002) from his surveys of grazing and mining habitats at Olympic Dam, South Australia provided data to indicate that reptile diversity, species richness and capture rates during December varied appreciably among years (1987 to 1991; 1994 to 1997, respectively). Capture rates for the six most commonly trapped reptile species outside mined areas (*Ctenotus regius, Ctenotus schomburgkii, Diplodactylus stenodactylus, Rhynchoedura ornata, Lerista labialis* and *Ctenophorus fordi*) differed appreciably, with no common pattern evident (Read 1992). Read (2002) indicated a similar level of variation in reptile abundance for his 'control' sites when he examined the effect of grazing on reptile assemblages in chenopod shrublands. These variations were of a similar order to that which we report here for commonly caught species from the same genera [e.g. *Ctenotus atlas* (70), *Diplodactylus granariensis* (346), *D. maini* (401), *D. pulcher* (432), *Rhynchoedura ornata* (124), *Lerista muelleri* (45) and *Lerista picturata* (89)] and others [e.g. *Strophurus assimilis* (141) and *Egernia depressa* (90)]. How (1998) reported that there were appreciable variations in the reptile assemblage of Bold Park, a remnant bushland (330 ha) on the coastal plain west of Perth, among years and although he normally caught all of the common species each year, abundance of these common species varied appreciably. Interestingly, year-to-year variation in the number of individuals caught in recently burnt areas was less than for the sites burnt more than 10 years earlier in the arid interior of Australia (Masters 1996). Masters (1996) reported appreciable variation in the number of species caught between years for the same season in long burnt sites. Dodd (1992) also reported considerable annual variation in the reptile community around a temporary pond situated in the Florida sandhills, and as the drought progressed the rarer species disappeared and the abundance of other species declined. Cowan & How (2004), in comparing reptiles trapped in March 1979, October 1980, October 2001 and March 2002 at Goongarrie Station, showed that the October 2001 and March 2002 assemblages were the most similar, and more similar to the March 1979 than the October 1980 assemblages.

Overall captures were less in the warmer months of 2001/02 than 2000/01 around Ora Banda, and this was most noticeable for geckos and skinks (Table 2). Mean minimum and maximum daily ambient temperatures were significantly warmer in December and January of 2000/01 than 2001/02 survey period. This might have accounted for the lower number of geckos and skinks caught in 2001/02. However, the mean minimum and

maximum daily ambient temperatures for September 2000 and 2001 were not significantly different but the number of geckos and skinks caught in 2000 was appreciably higher than 2001. This led us to conclude that factors other than ambient temperature, which we could not identify, could have also contributed to the year-to-year variation in catch rates. Interestingly, Brown & Shine (2002) reported considerable daily variation in activity levels for snakes in tropical Australia, but concluded that standard weather variables such as temperature, humidity and precipitation were poor predictors of activity.

It rained for a number of days during the second week of pit-trapping in January 2003 (total of 32.5 mm). It also rained in January 2001 (total of 6 mm) and 2002 (total of 12.15 mm), but not as heavily (Table 2). We believe the total number of individuals and species caught were less in January 2003 than in the two previous January surveys because reptiles were generally less active in the cooler days associated with the higher rain (Table 2). However, this rain may have caused the increased catch rates for a couple of species. The proportional number of termite eating specialist geckos (*D. pulcher*, *R. ornata*) was higher in January 2003 than in previous January surveys. The abundance of termites and possibly other invertebrates immediately after the rain may have made feeding relatively easy. We observed many swarms of termites active on the surface of logs and the leaf litter mid-morning on the first day after heavy rain. Most *D. pulcher* and *R. ornata* pit-trapped immediately after the heavy rain had engorged themselves and had distended abdomens from feeding on termites. These data suggest that these two termite specialist feeding geckos that can forage at lower body temperatures (Roberts 1998) were taking advantage of the available food resource, and were being caught in our pit-traps in higher numbers as a consequence. In contrast, catch rates for the diurnal, termite eating specialist skink *Egernia depressa*, and *Ctenotus uber* and *Ctenotus atlas* whose diets are also predominantly termites, were not higher after rain. The cooler ambient day temperature during the 3–4 days after rain possibly limited foraging opportunities for these skink species.

Can we misinterpret natural year-to-year variation as being caused by some stochastic event? Pianka (1996) compared lizard assemblages on the western edge of the Great Victoria Desert (L-area) for three periods (1966–68, 1978–79, 1989–92) and attributed changes in species richness and abundance between these periods to fires in 1968–69 and 1983. Fires probably were a major contributor to these changes, but in the absence of an understanding of 'normal' year-to-year variation, it is difficult to attribute all differences to fires. In addition, variations in the total number of captures (530 in 1966–68; 1565 in 1978–79; 1997 in 1989–92) would have also influenced estimates of species richness and abundance (Gotelli & Graves 1996, Thompson *et al.* 2003) as may have been the removal of all caught individuals from the study site during each sampling. Pianka (1996) also reported species diversity increased at another of his study sites (Redsands) between 1978–79 and 1989–92 and again suggested a fire in 1982 was a significant contributor to this increased diversity. The latter survey was more comprehensive (1436 individuals vs 3196 individuals) as a consequence of a higher surveying

effort. Variations in catch rates for some species between the two successive years at our Ora Banda study site exceeded those reported by Pianka where there are 10 years between survey periods. We are not suggesting that the fire had no impact on diversity or abundance at Redsands or L-area, as it clearly did, as much of the spinifex was destroyed and many of the small reptiles use spinifex as shelter and their primary foraging site in the Great Victoria Desert (Pianka 1986).

Masters (1996) in a study of the impact of fire on reptile abundance and species richness in Uluru National Park reported that relative abundance of reptile fauna on regenerating (from fire) plots changed over three years. During the third year of her investigation, Masters reported total abundance for the February survey period (1990) in the area burnt 12 years earlier declined significantly compared with the previous two years (1988 and 89), whereas a similar change was not evident in the area burnt some 2–4 years earlier. For species richness, the February survey in the third year (1990) was comparable with the first year (1988), but the number of species caught in the second year (1989) for the areas burnt 2–4 and 10–12 years earlier was higher. Masters (1996) suggested that as the total (vegetation) cover increased in recently burnt areas the number of diurnal species caught increased (although data supporting this claim were not provided). What is evident from Masters (1996) data is that there were considerable year-to-year variations in both total abundance and species richness for long burnt sites (controls). We know that abundance of captures is positively correlated with the number of species caught in arid and semi-arid habitats in Australia (Thompson *et al.* 2003), and the comparatively low number of individuals caught in the third year of Masters' surveying may have influenced the reported species richness values for that year or there may have been a real decline in reptile abundance. Therefore, some of the difference in species richness attributed to succession or vegetation cover was probably 'normal' year-to-year variation and a result of inadequate surveying.

Conclusion

A terrestrial faunal survey undertaken for the purposes of preparing an EIA can only describe the assemblage for a particular period in time. As activity patterns for reptiles and capture rates vary seasonally, terrestrial faunal surveys need to be undertaken in more than one season. In the Goldfields region of WA, surveys should ideally be conducted in spring, summer and autumn; and if this is not feasible then the surveys should be undertaken in September/October and January. Data from terrestrial fauna surveys can also be used to monitor rehabilitation success and impacts of disturbance on adjacent areas. This recommendation has obvious significant financial consequences for mining companies and other agencies that want to disturb the natural environment and arrange to have terrestrial faunal surveys undertaken to describe the faunal assemblage in the area to prepare an EIA. Similarly, government agencies undertaking faunal surveys of particular areas or regions for the purpose of zoning land for reserves or recording the biodiversity need to survey in more than

one or even two seasons, and need to understand that assemblages can change appreciably from year-to-year. We concur with the views of How (1998 pp. 148) who argued that 'an extensive sampling effort was required in both temporal and spatial scales before the composition of a herpetofaunal assemblage can be adequately determined'. This view is also supported by more recent data presented by Cowan & How (2004) for the Goldfields.

In most circumstances, the current level of knowledge cannot separate natural year-to-year variation in reptile assemblages from variations attributable to stochastic events such as fire, grazing, drought or unseasonally heavy rainfall. Long-term studies of variations in reptile assemblages are therefore required if we are to adequately interpret the impact that stochastic events have on particular areas. The extent of year-to-year variations in reptile assemblages will differ in accordance with climate, vegetation and topography. Such studies are therefore required in a range of habitats. Ideally, a Before-After-Control-Impact (BACI) experiment with appropriate replication is necessary to demonstrate the impact of stochastic events and how they differ from natural seasonal and year-to-year variations. Investigations such as those cited above that link temporal variations to fire or unusual rainfall events lack both adequate replication and 'before' data. However, it is not always possible to establish such experiments and alternative research designs are necessary. Underwood (1994) suggested a way around the problem of a lack of adequate 'before' data. Because natural variations recur repeatedly it may be possible to sample a range of randomly chosen replicates in undisturbed habitats to establish natural variance among times, locations and their interactions. These data could then be used for comparison with data collected 'after' at control sites and given no difference, then used as 'before' data to compare with the 'impact' data.

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Notes on ....

Capture rates of small vertebrates decrease as the pit-trapping effort increases at Ora Banda

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Abstract. Based on 27216 pit-trap nights, we measured catch rates for reptiles and mammals using bucket and pipe pit-traps over seven consecutive days for nine sites for eight trips over two years in the Ora Banda region of Western Australia. The number of individuals captured was highest for both mammals and reptiles on the first day that pit-traps were open. For mammals, catch rates declined over a period of four consecutive days and then remained at that level. All species were likely to be captured in the first two days of trapping days with the trapping strategy that we used. For reptiles, catch rates declined for the first four days then increased to a level similar to days 2 and 3. New species of reptiles were captured after the fourth day of trapping, so extended periods of pit-trapping increases the proportion of species in the assemblage that are captured, although the return on trapping effort declines.

Keywords: pit-trap, trap effort, reptile, mammal

Introduction

Moseby & Read (2001) reported that for a 10 day survey the last night of pit-trapping typically captured between one third and one half of the first night's catch. Their first full day of trapping yielded the highest number of captures, and nights 1–3 captured significantly more than nights 6–10. We examined whether capture rates for mammals and reptiles changed with successive trapping days, and whether these changes were influenced by using buckets or pipes as pit-traps for an intensive survey of the Ora Banda region, Western Australia.

Materials and methods

Study sites

We surveyed nine relatively undisturbed sites (Gimlet, Palace, Rose, Wendy Gully, Salmon Gums, Spinifex, Davyhurst, Security and Crossroads) in the gold mining region of Ora Banda (30° 27' S, 121° 4' E; approximately 50 km north of Kalgoorlie), Western Australia over a two year period. Ora Banda lies on Archaen granites that underlie lateritic gravel soils. The vegetation was

heterogenous, ranging from Eucalypt-Casuarina-Mulga woodlands interspersed with *Acacia*, to sparsely distributed spinifex (*Triodia* spp) and shrubs (*Acacia* spp) to dense shrubs (*Acacia* spp, *Atriplex* spp, *Allocasuarina* spp). Each of the nine sites represented a different vegetation type and was typical of the area (Mattiske Consulting Pty Ltd 1995).

Pit-trapping

All sites were pit-trapped on eight occasions between Sept 2000 and Apr 2002 (Sept and Dec 2000; Jan, Apr, Sept and Dec 2001; Jan and Apr 2002) using alternating 20 L PVC buckets and 150 mm PVC pipes (600 mm deep) with a 250 mm high x 30 m long fly-wire drift fences. Each site had eight rows of six pit-traps. All pit-traps were prepared before the study in June–July 2000. During each survey period, pit-traps were opened for seven consecutive days and cleared daily. In Sept, Dec and Jan survey periods, study sites were divided into two groups and surveyed in successive weeks. Most individuals were identified before immediately being released adjacent to their point of capture; a few specimens were vouchered with the Western Australian Museum. Recaptures have been included in the analysis. We report 27216 pit-trap nights of data.

Data analysis

We combined data for eight survey periods and used a repeated measures ANOVA, with days nested in seasons, which were nested within years with buckets and pipes as factors to determine significant differences among years, seasons, days and trap type for individuals and species. A post hoc Tukey test was used to examine differences among days.

We used a species accumulation curve for the January 2001 survey period to illustrate the capture rate of additional species of reptiles and mammals over seven days of surveying. More reptile individuals and species were captured during the Jan 2001 seven day survey than any other survey period, therefore these data represent the best possible capture rate for species in the area. The Beta-P non-linear regression model was then used to calculate a species accumulation curve from the data (Thompson *et al.* 2003).

Results

For mammal abundance there was no significant difference between buckets and pipes ($F_{1,16}$ = 3.04, P = 0.10), years ($F_{1,16}$ = 0.04, P = 0.84) or seasons ($F_{3,48}$ = 0.08, P = 0.97), but there was a significant difference among days ($F_{6,96}$ = 11.47, P < 0.001). For mammal species richness there also was no significant difference between buckets and pipes ($F_{1,16}$ = 2.17, P = 0.16), years ($F_{1,16}$ = 0.01, P = 0.91) or seasons ($F_{3,48}$ = 0.68, P = 0.57), but there was a significant difference among days ($F_{6,96}$ = 10.14, P < 0.001).

For reptile abundance there was a significant difference between buckets and pipes ($F_{1,16}$ = 34.74, P < 0.001), years ($F_{1,16}$ < 44.0, P < 0.001), seasons ($F_{3,48}$ = 40.7, P = 0.001) and days ($F_{6,96}$ = 14.06, P < 0.001). For reptile species there also was a significant difference between buckets and pipes ($F_{1,16}$ = 11.3, P < 0.001), years ($F_{1,16}$ = 36.4, P < 0.001), seasons ($F_{3,48}$ = 58.3, P < 0.001) and among days ($F_{6,96}$ = 15.1, P < 0.001).

Table 1

P-values from a post-hoc Tukey test of the differences in catch rates among consecutive pit-trapping nights. P-values in bold are significant at a < 0.05.

Days	2	3	4	5	6	7
Mammal abundance						
1	0.460	**0.018**	**0.C01**	**C.001**	**0.001**	**0.001**
2		0.780	**0.001**	0.086	**0.049**	**0.005**
3			**0.007**	0.819	0.695	0.222
4				0.255	0.371	0.853
5					1.000	0.952
6						0.985
Mammal species						
1	0.961	**0.043**	**0.001**	**0.004**	**0.001**	**0.001**
2		0.356	**0.001**	0.071	**0.019**	**0.001**
3			**0.043**	0.988	0.874	0.211
4				0.254	0.537	0.994
5					0.999	0.663
6						0.910
Reptile abundance						
1	**0.001**	**0.001**	**0.001**	**0.001**	**0.016**	**0.001**
2		0.909	**0.040**	1.000	0.503	0.999
3			0.462	0.897	**0.048**	0.991
4				**0.037**	**0.001**	0.122
5					0.523	0.999
6						0.250
Reptile species						
1	**0.001**	**0.001**	**0.001**	**0.001**	**0.021**	**0.001**
2		0.443	**0.030**	1.000	0.443	1.000
3			0.879	0.516	**0.003**	0.310
4				**0.041**	**0.001**	**0.015**
5					0.374	1.000
6						0.591

The catch rates for mammals for day 1 differed significantly from catch rates for most successive trapping days, for both abundance and the number of species captured (Table 1). Similarly, the catch rate for reptiles for day 1 differed significantly from subsequent days for both abundance and number of species captured. Day 4 generally had the lowest catch rates for both mammals and reptiles (Figs 1, 2). A significantly
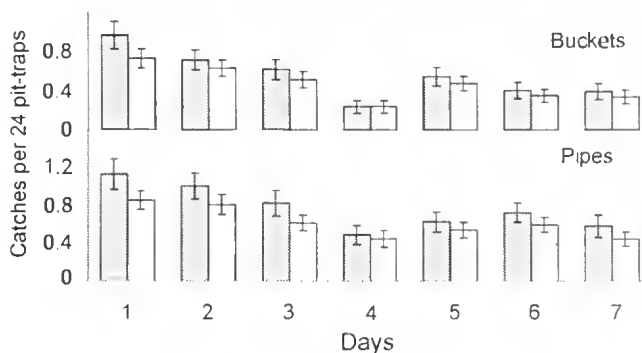
Figure 1. Catch rates for mammals for consecutive nights at Ora Banda using buckets and pipes. Abundance in grey fill and species in clear fill; values are mean with one se.

lower number of reptile individuals and species were captured on day 4 than days 1 and 2, and day 5 (Fig 2), and day 6 for reptile species (Table 1).

The species accumulation curve for the January 2001 survey period for reptiles (Fig 3) shows that most, but not all species, were captured in the first two days of trapping. All six species of mammals were captured on the first day during this January survey period.

Discussion

Moseby & Read (2001) reported for three sites in the arid interior of northern South Australia that for reptiles day 6 in the grazed area was the first day in which catch rates were significantly lower than day 1, compared to day 5 for pastoral areas, and day 2 for mined areas. Their catch rates continued to decline over 10 days of trapping. The pattern for reptile captures in natural habitats at Ora Banda differed among consecutive days. Day 1 captured the highest number of reptiles, with a progressive decline to day 4, after which the catch rate increased. The pattern was the same for buckets and pipes. Why there was a decline and a subsequent increase was not obvious. Some species of reptiles are attracted to freshly dug soil (e.g. *Varanus eremius*, pers. obs), and this might account for the higher initial catch rate (e.g. day 1). This is an obvious reason for leaving a period between when pit-traps are
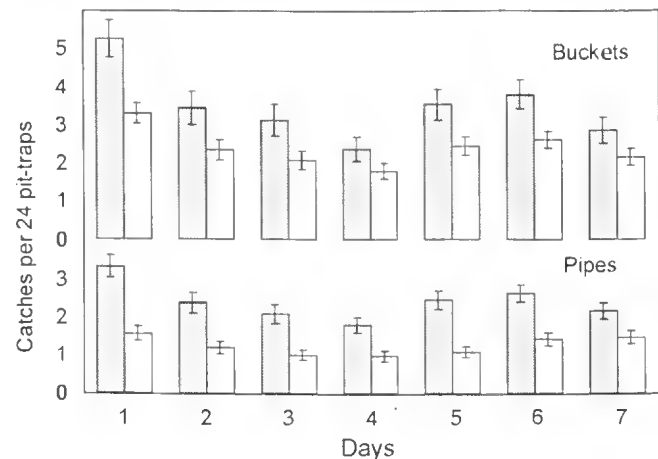
Figure 2. Catch rates for reptiles for consecutive nights at Ora Banda using buckets and pipes. Abundance in grey fill and species in clear fill, values are means with one se.
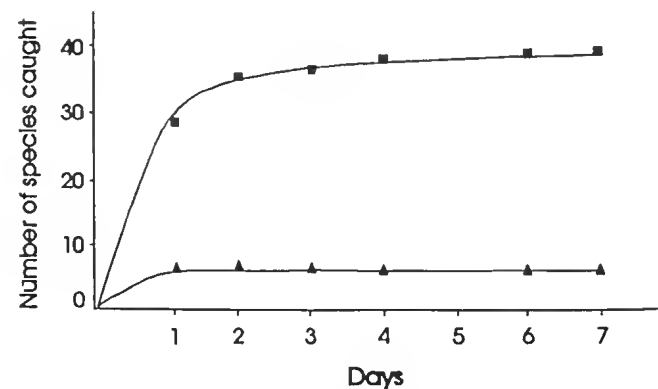
Figure 3. Species accumulation curves for Jan 2001 survey period over seven consecutive days. Squares (reptiles) and triangles (mammals) are actual data points; reptile species accumulation curve is calculated using the Beta P model.

dug into the ground and when they are first opened for the purposes of sampling the reptile assemblage.

Mammal captures declined progressively for the first four days, increased a little and remained at that rate thereafter. As for reptiles, there was no difference in the pattern between buckets and pipes. These data suggest that mammals are either learning to avoid pit-traps, are moving away from the area, or are dying as a result of being captured.

Although catch rates generally declined over the first four days, new reptile species were still being captured after day 4. We have captured 51 species of reptiles around Ora Banda (9 sites), although we only captured 39 species during Jan 2001. With lower captures during other survey periods, additional trapping effort would be required to catch the same number of species. Our survey data indicate that unless intensive surveys are carried out or surveys are undertaken during spring, summer and autumn, then all species will not be captured within seven days using our trapping strategy (also see Thompson *et al.* 2003). Therefore, if the objective of the terrestrial fauna survey is to record all available species in the area, a much greater trapping effort than was

applied here is required. It was evident that at least for the first seven days of a survey, both mammal and reptile catches will decline for the first four days. Mammal catches will stay low after the fourth day, around 40–50% of the first days catch, but reptile catch rates will increase to a level similar to day 2, at least at Ora Banda.

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Range extension for the Perentie, *Varanus giganteus* (Squamata: Varanidae)

Notes on ....

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Abstract. Three recent sightings of *Varanus giganteus* increase its recorded geographical distribution in a south-westerly direction. These sightings may represent previously unrecorded populations, indicate a range extension, or in one instance a translocation. If these are disjunct populations from the published distribution to the north-east, then there may be a strong case for affording special protection to their habitat to protect these populations.

Keywords: *Varanus giganteus*, Perentie, geographic range, Western Australia

Introduction

The habitat of the Perentie, *Varanus giganteus*, is described by Cogger (1992) as the 'arid interior of Australia from far western Queensland through central Australia to the coast of WA' (p 362), where it inhabits deep crevices and burrows in rocky outcrops, and forages widely on adjacent sandy desert areas. King *et al.* (1989) reported that most of the *V. giganteus* they observed on Barrow Island were on the beach. In the Cape Range National Park, where Perenties are relatively abundant, they inhabit the coastal dunes, sand plains and rocky inland range (Heger 2000). Pianka (1994) recorded *V. giganteus* in the red sand-ridges of the Great Victoria Desert in areas predominantly vegetated with spinifex far away from rock outcrops.

Distribution maps for *V. giganteus* typically include the sandy desert areas of central Western Australia stretching from the west coast to the eastern north-south South Australian and Northern Territory borders and into the western edge of Queensland (Storr *et al.* 1983; Cogger 1992; Wilson & Knowles 1992; Western Australian Museum *FaunaBase* http://www.museum.wa.gov.au/faunabase/prod/index.htm). We report here three recent sightings that are outside the published geographical distribution for this goanna. We also summarise other sightings that increase its published distribution.

Observations

On 3rd October 2001, about 1400 hr, we observed a Perentie foraging about 2 km north-west of the Aurora Range, Western Australia (30° 19'S, 119° 43'E) in a eucalypt woodland with a chenopod shrub understorey (Fig. 1). We estimated the specimen to be about 1.4 m in total length (it was not caught). Mr T. Trent of the Western Australian Department of Agriculture observed a Perentie on the road 10 km east of Kununoppin (31° 08'S, 117° 59'E) that was in the process of consuming an adult Western Bluetongue, *Tiliqua occipitalis*, on 17th October 2001, at 1408 hr. This Perentie was about 1.4 m in length. This specimen was probably living in a large adjacent nature reserve that was surrounded by farmland. Mr B. Eidenmüeller reported (pers. comm.) sighting a *V. giganteus* (> 1.8 m total length) on 12th January 2001, at 1100 hr, about 2 km north of the bridge over the Murchison River on the North-West Coastal Highway (27° 48'S 114° 41'E). These three records are a considerable distance south and south-west of the published range for *V. giganteus* (Fig. 2).

In addition to the above observations, Pianka (1994) reported seeing two *V. giganteus* crossing the road between Menzies and Leonora (30° 01'S 121° 10'E; 46 km S of Leonora). Ray Hart (pers. comm.) found a dead Perentie on the same road in this vicinity in December 2000, and Dell *et al.* (1988) reported a *V. giganteus* on Goongarrie station. Dell *et al.* (1985) reported sighting *V. giganteus* at Mt Jackson and Bungalbin Hill, indicating a range extension of approximately 100 km. Chapman and

Figure 1. *Varanus giganteus* seen near the Aurora Range.
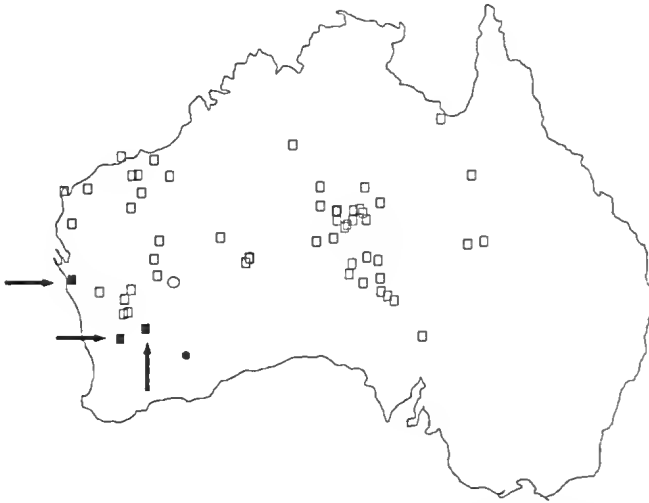
Figure 2. Distribution of *V. giganteus* based on specimens vouchered in Australian museums (□), Pianka's Red Sands study site (○), the 'Norseman' record (●) and the three range extensions (■) reported here.

Pronk (1997) subsequently reported seeing a *V. giganteus* in their fauna survey of the Helena and Aurora Ranges. Ecologia (2001) reported seeing *V. giganteus* on the southern end of the Aurora Range (Bungalbin Hill; 30° 24' S, 119° 38' E) and at Mt Jackson (30° 12' S, 119° 06' E) some 40 km to the west of our sighting. These geographic records for *V. giganteus* are not reflected in the Western Australian *FaunaBase*, and need to be incorporated into geographic distribution maps (e.g. Cogger 1992; Wilson & Knowles 1992).

Figure 2 indicates the recorded locations of *V. giganteus* in all Australian museum collections and the extension to its published distribution represented by these three specimens. The Australian Museum records an individual at Norseman (32° 12'S, 121° 47'E) which we believe is either a recording error or a relocation as extensive investigations in the general area have failed to sight another *V. giganteus*.

Discussion

Pianka (1994) reported an increase in abundance of *V. giganteus* around his 'Red Sands' study site (28° 12'S, 123° 35'E) in the Great Victoria Desert between 1966 and 1993. He speculated that the Perentie could be expanding its geographic range southwards and eastwards.

There is about 150 km between the Perentie population in the Menzies – Goongarrie area and those in the Mt Jackson – Aurora Range area. There is a substantial well vegetated sand plain to the north and east of the Aurora Range that would separate *V. giganteus* in this area from those reported in the Menzies – Goongarrie area. It is not known if the population in the Mt Jackson – Aurora Range area is disjunct from those around Goongarrie and further north, or whether they are present on the sand plain.

The sighting of a *V. giganteus* near Kununoppin is approximately 300 km south-west of those reported in the sand plain area in the Menzies – Goongarrie area. This individual is further south-west than any shown in

the distribution maps of Storr *et al.* (1983), Cogger (1992) and Wilson & Knowles (1992) for Western Australia. Smith *et al.* (1997) reported on the vertebrate fauna in nine remnants of native vegetation ranging between 10 and 1030 ha in the area between Kellerberrin and Trayning, which is approximately 40 km south-west of this sighting, without seeing a Perentie. Smith *et al.*'s (1997) extensive survey caught over 11,000 animals of 51 species during 65,000 trap-nights, suggesting that if *V. giganteus* were present they would have been seen or caught. Many of the small native vegetation reserves in the wheatbelt have been surveyed, and to our knowledge none is reported to contain *V. giganteus*. These data suggest that this individual represents either a significant extension to the species' published geographic range, in which case this large, wary and cryptic reptile has gone unrecorded in this area for many years, or the species has recently moved into the area or it has been a translocation.

The sighting of a *V. giganteus* about 2 km north of the bridge over the Murchison River on the North-West-Coastal Highway is approximately 200 km west of the nearest record for this species in the Western Australian Museum collection (closest is slightly south of Yalgoo). The Riverside station owner on the southern bank of the Murchison River, near where Eidenmüeller saw the Perentie, indicated that he has seen large goannas on his property for a number of years (pers. comm.). This area is open woodland with a dense understorey in some areas. This information suggests there is a small population of *V. giganteus* in the area. The area between this small population and Yalgoo is mostly pastoral leases that are sparsely grazed by sheep. It is not known if there are other small populations of *V. giganteus* in the intermediate area.

Conservation implications

Being a large carnivorous lizard (up to 880 mm SVL; King & Green 1993) Perenties are mostly likely to occur in low population densities unless there is an unusually high abundance of prey (e.g. Barrow Island). It is probable then that the population of *V. giganteus* in the range extension areas where we have reported them is small. Small populations are vulnerable to extinction when habitats are disturbed. The Aurora Ranges is an area of increasing mining activity, farming surrounds the nature reserve east of Kununoppin, and there are grazing and tourist developments along the Murchison River to the east of the sighting by Eidenmüeller. Small populations of *V. giganteus* might also exist in other small remnants of native vegetation between these three locations and the published distribution to the north and east.

It is not unusual to find isolated populations of a particular of reptile within its published geographical distribution as few species are evenly spread across their known range. However, our three records represent extensions to the published distribution and at least two are likely to be disjunct populations separated by agriculture from its known range to the north and east. If we adopted the precautionary principle, then there is a *prima facie* case for affording a level of special protection to these habitats, until more extensive surveys of the area between the published distribution and these three

sighting have been undertaken. If there are only a few habitats that support these disjunct populations of *V. giganteus*, then appropriate habitat protection strategies should be put in place.

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Description of sternal glands in Western Australian *Sminthopsis* and *Ningaui* (Marsupialia: Dasyuridae)

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Abstract

We have identified a cutaneous secretory gland in the gular (throat) area of the small carnivorous marsupials, *Sminthopsis* and *Ningaui* spp, and in all other genera of dasyurid marsupials that occur in Western Australia. The gland is apparent in both sexes of *Sminthopsis* and *Ningaui*, and develops with maturity. It contains both sebaceous and apocrine sudoriferous glands, and is similar in gross and histological structure, and probably function, to the sternal gland previously described for other dasyurid marsupials, although it is located more anteriorly in the gular region.

Keywords: gland, epidermal, sternal, gular, *Sminthopsis, Ningaui,* dasyurid, marsupial, histology

Introduction

The skin of marsupials, like that of other vertebrates, has glands of varying functions (Dawson *et al.*, 1989). Scent-producing secretory glands are common, suggesting an important role in olfactory communication. Russell (1985) described scent glands in 63 marsupial species from 40 genera. These include sternal, paracloacal (anal, or paraproctal), pouch, auricular, oral and frontal glands, as well as nasal vestibular glands, sebaceous and serous ocular glands, and lachrymal glands.

Sternal glands are widespread in marsupials; their presence is often indicated in the sternal region by a bare patch of skin, and/or discolouration of the surrounding fur. They typically are larger in adult males, and gland size and secretory activity change seasonally (Dawson *et al.*, 1989). The sternal gland consists of both sebaceous and apocrine sudoriferous cutaneous glands, which are typically larger and more active than the adjacent cutaneous glands. The sternal gland hairs, especially for sexually mature animals, sometimes appear moist with the glandular secretion (*e.g.* Bolliger & Hardy, 1945; Mykytowycz & Nay, 1964; Woolley, 1991). Sternal glands are used during marking behaviour to spread the sternal secretion on objects in the environment (Russell, 1985; Toftegaard & Bradley, 2003) *e.g.* scent-marking by *Antechinus* (Woolley, 1966).

Routine curatorial examination of specimens of *Sminthopsis* species in the Western Australian Museum mammal collection revealed a cutaneous secretory gland in the gular area that develops in both males and females as they become sexually mature. We report here how further systematic examination of specimens has shown that this gland appears to be present in essentially all Western Australian species of *Sminthopsis*, and genera of dasyurids, and is homologous with the previously described sternal gland of other dasyurids.

Methods

We examined specimens of primarily *Sminthopsis* and *Ningaui* spp, but also some individuals from species of all genera of the sub-families of the Dasyuridae that are present in Western Australia, for sternal glands. Observation of Museum specimens was made using a binocular microscope. The fur of spirit specimens (preserved in formalin and then stored in 75% ethanol) was brushed into a natural orientation for examination. We intended primarily to only survey whether or not the gland was present in all species of dasyurid marsupials in Western Australia; this could have been indicated by bare skin or complete gland development. The sex and sexual maturity of specimens with sternal glands were noted. We designate animals as sexually mature when for females there was development of pouches, teats or attached young, and for males from knowledge of season of reproductive activity of species, size of animal and size of testes.

Sections of sternal glands were removed from formalin-fixed, alcohol-preserved specimens of some species for histological study by paraffin sectioning. Sections of 6 μ were examined with a variety of stains, including haematoxylin & eosin, and Heidenhain's azan (Humason 1979), to identify different stages of development of the gland and compare the structure of the gland between sexes and between species.

Results

Examination of specimens of the thirteen *Sminthopsis* and three *Ningaui* species in the Western Australian Museum mammal collection consistently revealed a cutaneous secretory gland in the gular area (Table 1). This gland is apparent in both sexes, and develops as the animal becomes sexually mature. Further examination of other genera of dasyurids that occur in Western Australia revealed a similar gland in all of the species examined (Table 1).

Table 1

Species of Western Australian dasyurid marsupials that have been examined, and location of gland (g = gular, s = sternal, gs = extending from gular to sternal area). Phylogeny after Krajewski *et al.* (1994). Registration numbers are for Western Australian Museum specimens, except SAM is a South Australian Museum specimen.

Subfamily	Genus	Species	Registration Number	Gland location
Sminthopsinae	*Antechinomys*	*laniger*	M36859 ♀	GS
	Ningaui	*ridei*	M44971 ♂, M52235 ♀	G
	Ningaui	*timealeyi*	M51370 ♂, M45076 ♀	G
	Ningaui	*yvonneae*	M47074 ♂, M47199 ♀	G
	Planigale	*ingrami*	M52047 ♂	G
	Planigale	*maculata*	M30874 ♂	G
	Planigale	sp nov	M52212 ♂	G
	Planigale	sp nov	M51417 ♀	G
	Sminthopsis	*butleri*	M7158 ♀	–
	Sminthopsis	*crassicaudata*	M47112 ♂, M44147 ♀	G
	Sminthopsis	*dolichura*	M47230 ♂	G
	Sminthopsis	*gilberti*	M1179 ♂	G
	Sminthopsis	*granulipes*	M24119 ♂	G
	Sminthopsis	*griseoventer*	M52167 ♂	G
	Sminthopsis	*hirtipes*	M41983 ♂ M21920 ♀	G
	Sminthopsis	*longicaudata*	M24530 ♂	G
	Sminthopsis	*macroura*	M51361, M23560 ♀	G
	Sminthopsis	*ooldea*	M28451 ♂	G
	Sminthopsis	*psammophila*	M23229 ♂	G
	Sminthopsis	*virginiae*	M21996 ♂	G
	Sminthopsis	*youngsoni*	M46745 ♂	G
Dasyurinae	*Dasycercus*	*cristicauda*	M48487 ♂	G
	Dasycercus	*hillieri*	SAM M15805 ♂	G
	Dasyurus	*geoffroii*	M53756 ♂	S
	Dasyurus	*hallucatus*	M48847 ♂	S
	Dasykaluta	*rosamondae*	M47752 ♂	G
	Parantechinus	*apicalis*	M36796 ♂	GS
	Pseudantechinus	*ningbing*	M12368	GS
	Pseudantechinus	*roryi*	M34304 ♂, M29372 ♀	GS
	Pseudantechinus	*woolleyae*	M47636 ♂, 48112 ♀	GS
Phascogalinae	*Antechinus*	*flavipes*	M52169 ♂, M52243	GS
	Phascogale	*tapoatafa*	M24617 ♂, M11171 ♀	GS
	Phascogale	*calura*	M20937 ♂	GS

The gland is most obvious in sexually-active males, but it is also present in juveniles and sexually-active females. However, Museum collection specimens of females with a fully developed gland are rarer than are males with a fully developed gland. The gland first appears as a bald area of skin on the throats of juvenile animals, hidden beneath the fur. The skin develops a 'goose-pimply' texture as the gland matures, and is swollen with a folded appearance in the fully mature gland (Fig 1). The gland appears first in the gular area but extends as it develops toward the sternal area. Discolouration of the fur around the gland was often observed.

Histological examination of the gular glands identified both sebaceous and apocrine sudoriferous glands. Early stages of development of the gland showed little or no evidence of hypertrophy of the precursor elements, with small numbers of sebaceous gland cells aggregated around hair shafts. Simple tubular (non-coiled or branching) glands lying deeper in the subcutaneous tissue are putative precursor elements of the sudoriferous glands. Intermediate stages of development of the gland showed thickening of the dermal and subcutaneous layers along with pronounced hair follicle loss. The sebaceous glands were hypertrophied into large simple acinar sacs, which opened directly to the skin surface via the former root sheath of the hair. These accounted for most of the epidermal thickening. The sebaceous glands appeared quite active, with secretion products evident in their lumen. Some hypertrophy of the sudoriferous gland was also evident. For the fully-developed gland, the sebaceous glands were similar in extent to the intermediate stage but in many cases the acini have become lobulated, with each lobe sharing a single opening to the surface of the skin. The sudoriferous glands had hypertrophied and the resultant coiled tubular glands formed discrete cords of glandular tissue oriented deep to the surface. Their secretory cells were truncated pyramidal cells with spherical nuclei that form a single layer. Secretory products of these tubular cords entered ducts located just below the sebaceous gland acini. There was some evidence that these ducts open into the pilo-sebaceous canal.

Discussion

Although Green (1963) did not report any enlarged or specialized sternal gland in *Sminthopsis crassicaudata*, we have identified a cutaneous gland in *Sminthopsis* species, but located in the neck rather than the chest area. With

Figure 1. Fully-developed gular gland of a male *Ningaui ridei* (M44971).
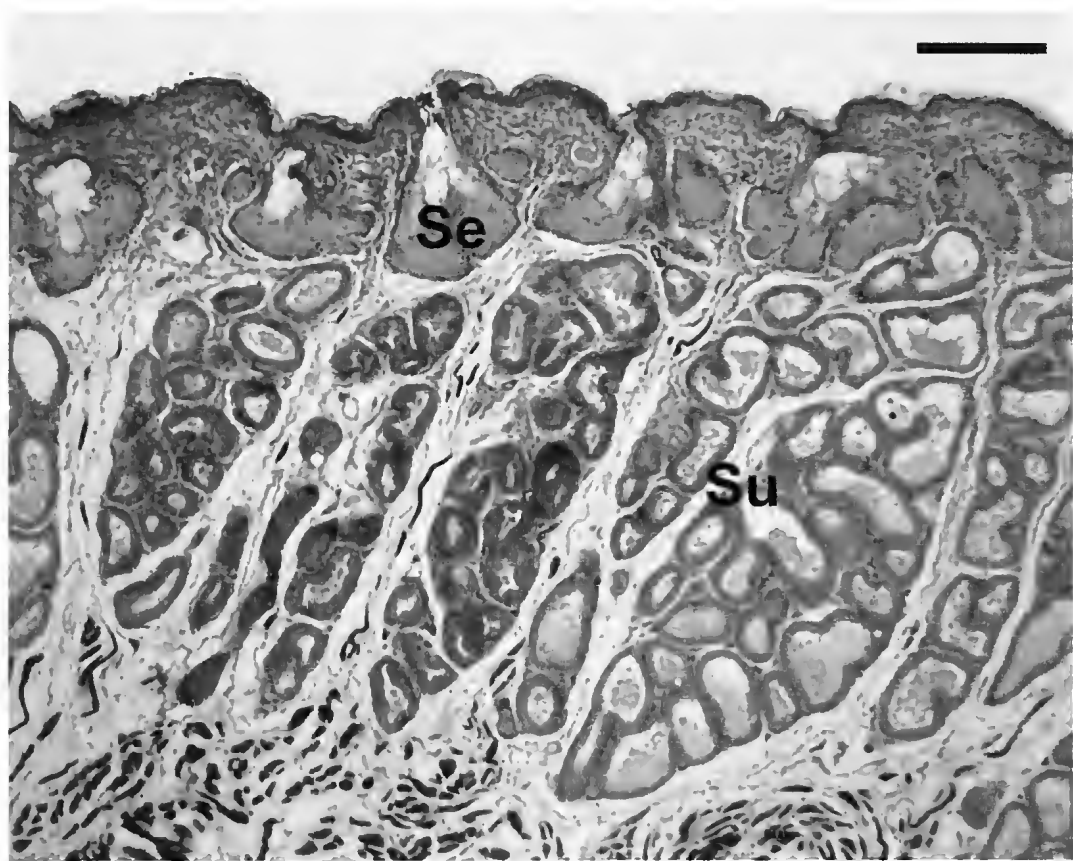
Figure 2. Fully developed gular gland in *Sminthopsis ooldea* (WAM 28451). The subcutaneous layer is thickened, with sebaceous glands (Se) that in many cases have become lobulated, with each lobe sharing the one opening to the surface of the skin, and sudoriferous (Su) glands that have hypertrophied with their resultant coiled tubular glands forming discrete cords of glandular tissue oriented deep to the surface (their ducts appear to open into the pilo-sebaceous canal). Scale bar: 200 μ.

enlargement of the gland it often extends down to the sternal area. We have confirmed that this gland is present in all species of *Sminthopsis* and *Ningaui* found in Western Australia, and it is found in representatives of all of the Western Australian subfamilies within Dasyuridae (Table 1). It would appear to be generally present in both male and female dasyurid marsupials. Previously, sternal glands have been noted in the following dasyurid species; *Phascogale tapoatafa* (Cuttle 1978), *Planigale maculata* (Van Dyck 1979), *Dasyuroides byrnei* (Aslin 1974), *Antechinus stuartii* (Woolley 1966), *Dasykaluta rosamondae* (Woolley 1991) and *Planigale tenuirostris* (Andrew & Settle 1982). Bourne (1934) and Ford (1934) re-described the pre-sternal/sternal gland of the numbat (*Myrmecobius fasciatus*) after Beddard's (1887) original description. Stoddard & Bradley (1991) and Bradley & Stoddard (1993) described the equivalent gland of the sugar glider *Petaurus breviceps* as a gular gland.

The sternal gland that we describe for small dasyurid marsupials is in the gular area rather than on the sternum, and is often obscured by fur. The bald sternal gland of *Sminthopsis* lacks the specialized sternal gland hairs (osmetrichia) of *Antechinus stuartii* (Toftegaard & Bradley 1999). The gland appears to be most fully developed in sexually mature males, and is present in females of most species examined although not so obvious. This may be an artifact of collectors being unwilling to collect females with young, or females with young may be less trappable (if that is the period of full development of the gland), or the gland may atrophy quickly after the reproductive period, or it might not ever develop as fully as in males. However, Aslin (1974) described a well developed sternal gland for female *Dasyuroides byrnei* with unweaned young, in captivity.

The external structure of the sternal gland appears the same for both sexes, for all species of *Sminthopsis* and *Ningaui*, and for all of the other genera in which the gland has been found. Histological study of the sternal glands identified both sebaceous and apocrine sudoriferous glands, as has been reported previously for sternal and some other glands in various marsupials (Bourne, 1934; Ford, 1934; Bolliger & Hardy 1945; Green, 1963; Stoddart 1980; Russell, 1985). The poorly developed system of both sebaceous and sudoriferous glands in immature specimens develops progressively with age. This development of the sternal gland is accompanied by some hair loss, making the glandular area more obvious.

The function of the gular gland of *Sminthopsis* and *Ningaui* is unknown, but like the cutaneous glands of other dasyurids (and other marsupials) it is probably important for olfactory communication between reproductively mature individuals. Woolley (1966) described the development of the sternal gland of sexually mature *Antechinus* and its use for marking objects. Aslin (1974) described scent marking of the substrate and/or objects during sand-bathing for the kowari *Dasyuroides byrnei*. *Planigale maculata* (Van Dyck 1979) has also been described to sternal rub. Sniffing of the neck region by conspecifics has been described for the mulgara *Dasycercus cristicauda*, the kowari *Dasyuroides byrnei*, the Eastern quoll *Dasyurus viverrinus* and the Tasmanian devil *Sarcophilus harrissii* (Aslin 1974; Eisenberg & Golani 1977; Eisenberg *et al.* 1975). Sternal

rubbing of objects and the substrate by *Sminthopsis crassicaudata* (Ewer 1968a,b) and *Ningaui* (Croft 1982) presumably deposits secretions of the gland for a similar olfactory identification role. Further study is needed to ascertain the timing of the development of the gland in females, the function of the gland, and whether the presence of the gland is an indicator of reproductive condition in *Sminthopsis* and *Ningaui* spp.

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Cataloguing biological surveys within Western Australia: the Pilbara experience

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Abstract

This paper details a project that was undertaken with the aim of documenting and reviewing all past biological survey work undertaken in the Pilbara bioregion of Western Australia. Bibliographic-style information was collated for 200 reports, with a further 589 identified for the bioregion. This descriptive information was then made available to the general public through a World Wide Web interface. The project did not achieve all of its aims, but has successfully listed details of the 200 reports, provides an additional resource for government assessors and also provides some context for biological surveys being undertaken in the Pilbara. As a case study, the project is a successful prototype knowledge management tool, a proven use for Internet deployment and has identified a wide range of 'grey' literature. It also has highlighted two issues that managers of biological survey data should consider; namely those of quality and ongoing data capture.

Keywords: Biological surveys, database, Pilbara, Western Australia

Introduction

There appears to be a general desire on behalf of global, national and state organisations to integrate a range of environmental data. The United Nations "Agenda 21" document, which is proposed as a blueprint for addressing environment and development issues into the 21st century, indicates that while considerable data exists, "more and different types of data need to be collected, at the local, provincial, national and international levels" in order to increase the capacity for making informed decisions concerning the environment (UNCED 1992, Chapter 40). The United Nations have instigated a number of projects, such as the Global Resource Information Database (UNEP 1996) to help achieve that aim.

The United Kingdom Royal Society recently recommended that "The scientific community needs urgently to emphasise synthesis that makes otherwise scattered data more readily available and more useful..." (The Royal Society 2003, pg 6). In Western Australia, the Environmental Protection Authority (EPA) in Guidance Statement No. 56 (EPA, 2003) states that "...terrestrial biological surveys will be made publicly available and will contribute to the bank of data available for the particular region..." (EPA 2003, pg 4). This followed "Position Statement No. 3" (EPA 2002), which noted that a state-wide biological 'bank of data' would aid our understanding of biodiversity and the Environmental Impact Assessment (EIA) process. Specifically, the EPA indicated that such a database would lead to:

- improved decision making;
- reduced costs for EIA; and
- conservation of biodiversity (EPA 2002, page 14).

The Western Australian environmental community is aware of how important this type of database would be to the industry. At a workshop held in April 2002, co-ordinated by the Royal Society of Western Australia, a number of presenters spoke of the need for co-ordination between existing custodians of such biological data sources (Thompson 2002 and Thompson & Withers 2002).

In June 2000 the Pilbara Iron-ore Environmental Committee (PIEC) released a tender for a project to document and review all past biological survey work undertaken in the Pilbara region of Western Australia. PIEC is an association of private mining companies and government organisations formed to foster the exchange of environmental and sustainable development knowledge and technologies among constituent members. PIEC members in 2000 included BHP Billiton, Hamersley Iron, Hope Downs Management Services, Robe River Iron Associates as well as the Departments of Conservation and Land Management (CALM), Environmental Protection (DEP), Resource Development (DRD) and Minerals and Energy (DME).

The project aimed to create a comprehensive bibliographical-style database containing descriptive information about all biological surveys carried out in the Pilbara. It should be noted that the project did not aim to collate the results of these projects (*i.e.,* trapping results or vegetation assemblages) into a single database. The project was perceived to have a range of uses for the PIEC members and the general public, which were documented in the objectives. These objectives were to:

1. provide a regional and local context for contemporary survey work being undertaken in the bioregion;

2. minimise duplication of effort among companies undertaking surveys;

3. list historical surveys;

4. provide an additional resource for researchers and assessment officers from government departments;

5. maintain a current listing of document authors; and

6. become a one-stop reference point for the identification of all biological surveys undertaken in the Pilbara, rather than the current situation where reports are scattered throughout the libraries of PIEC members.

The project was spatially limited to the Pilbara biogeographic region as defined in the Interim Biogeographic Regionalisation for Australia (Environment Australia 2000). This was further limited to the Pilbara mainland and associated island areas above the low water mark; thereby excluding marine surveys. Consequently, all publications reporting on flora, vegetation (including mangroves) and vertebrate fauna were to be captured by this project.

Methods

The June 2000 tender required the review of all previous biological surveys undertaken in the Pilbara and the collation of a range of descriptive information. The second phase involved the migration of the collated information to an on-line environment at the Western Australian Herbarium.[1]

Phase One: Identification and Collection of Data

Biota Environmental Sciences (Biota) were the successful lead tendering organisation for the PIEC project. Data collection occurred during late 2000 and early 2001 and consisted of an extensive literature search, followed by the collation of descriptive information from identified and relevant reports. Reports were sourced from the libraries of Biota, Hamersley Iron, BHP Billiton and the DEP. Of particular use to the project were two publications: "A bibliography and research inventory of vertebrate fauna in Western Australia" (CALM 1984); and "Bibliography of location-based biological studies in Western Australia" (CALM 1994).

The Spatial Metadata Management System (SMMS) application, produced by Intergraph, was used to collect the descriptive information for each report in a digital format. While SMMS was designed to manage descriptive information for spatial datasets, it also had the ability to record data such as bibliographic, taxonomic and methodological data. The software utilised an underlying Microsoft Access database for data storage.

One person (the author) was responsible for data collection to ensure consistency in the capture of descriptive information. The information collected included items such as:

- bibliographic information, *e.g.*
  - o title,
  - o originator,
  - o publication date; and
  - o abstract;

- biological information, *e.g.*
  - o methodologies used; and
  - o any taxonomic references;
- spatial extents of the survey; and
- keywords identifying the nature of the survey.

A list of keywords was generated during the initial stages of the project, and supplemented through in iterative process with the PIEC membership. The keywords were collected to provide a means of searching the database for publications related to particular areas of interest, without having to either read or search through detailed information for each report.

A discussion paper was submitted to the PIEC in May 2001 (Biota Environmental Sciences 2001a) and a final report was provided to the PIEC in June 2001 (Biota Environmental Sciences 2001b). A copy of the underlying Microsoft Access database was also supplied on CD-ROM with the final report.

Phase Two: Migration to the On-Line Environment

The second phase of the project commissioned in June of 2002 with the aim of making the data available via the World Wide Web (WWW) through the existing web site of the Western Australian Herbarium (a division of CALM). The first release of data onto the WWW was aimed at demonstrating to PIEC that the data could be made web-accessible.

The descriptive information stored in the database went through a number of processing steps to meet the requirements of the existing databases at the Western Australian Herbarium. Initially the data were exported from SMMS into a plain text format file. The file was subsequently processed in Microsoft Excel to remove special characters and then exported to a text format file. Several "search and replace" operations ensured the file was properly delimited and was supplied to the Herbarium in August 2002. The data were subsequently uploaded to the Herbarium databases and were released onto the WWW in October 2003, marking the end of the second phase of the project.

Results

Phase One: Data Collection

The data collection resulted in the identification of 789 biological survey reports. All 789 had the title information included in the database, although due to time and budgetary constraints, only 200 of these reports were sourced and had descriptive information entered into the database. It is probable that these 789 reports do not represent the entirety of biological surveys undertaken in the Pilbara.

The final report (Biota Environmental Sciences 2001b) included the following recommendations:

- appointment of CALM as the data custodian;
- hosting of the data using Western Australian Herbarium infrastructure;

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[1] Author's note: At the time of submission in July 2004, the project had proceeded to a third phase where additional reports were being entered by CALM staff into a purpose-built database.

- maintenance to be undertaken annually;
- no charges to be made for accessing the resultant web site;
- registration of users to be undertaken via the web site; and
- keywords to be reviewed and refined in the future.

Phase Two: Migration to the On-line Environment

In the second phase of the project, several of the recommendations of the first phase were implemented. CALM accepted its role as custodian, and commissioned a project to host the data at the Western Australian Herbarium. A subset of the descriptive information held in the database can be accessed through the web site http://science.calm.wa.gov.au/projects/pilbaradb/ and is available to the general public free of charge.

Discussion

The project has achieved one of its objectives, partially accomplished two additional ones but has failed to meet the remaining three. Of the 789 surveys identified during the project, only 200 (25%) were sourced and had descriptive information compiled. Each of the project objectives is discussed in the following sections.

1. Providing both regional and local context

The database provides a regional and local context for biological survey efforts. Any party that is proposing to undertake a biological survey in the Pilbara can carry out a search of the database using the existing web interface. Proponents, such as the major mining companies in the Pilbara, can investigate biological survey effort already undertaken in specific areas before commissioning additional work. Since it is unlikely that any single person can be aware of the entire body of work present in this database, this search mechanism represents an effective information management tool.

A current limitation of the database is that the entire suite of reports for the Pilbara has not been captured.

2. Removing duplication of effort

It is possible to see how the results of this project can remove duplication of biological survey efforts can be avoided through a simple search of an area prior to commissioning new surveys. However, as the database is not an exhaustive list of all biological surveys, and the level of use of this database is not known, it is not likely to be achieving this objective.

3. Listing historical surveys

There was no time limit placed on the reports that were to be entered into the database. The earliest report listed in the database is dated 1828, by A. Cunningham, entitled "A few general remarks on the vegetation of certain coasts of Terra Australia, and more especially of its north-western shores". The latest reports were sourced in the year 2000 (26 reports in the database were published in this year). Most of the reports have been published in the last two decades (Figure 1).

4. Providing additional resources for researchers and for government assessors

Achieving this objective is hampered by an incomplete data set. However, for those researchers and assessing officers that are aware of the project and the web interface, it is a quick method of accessing a substantial quantity of privately published reports that are generally not accessible using the established scientific bibliographic databases. For example, research projects such as that undertaken by Fraser *et al* (2003) could have used the database to analyse a larger cross-section of the methodologies used in biological survey reports. The project has therefore partly achieved this objective.
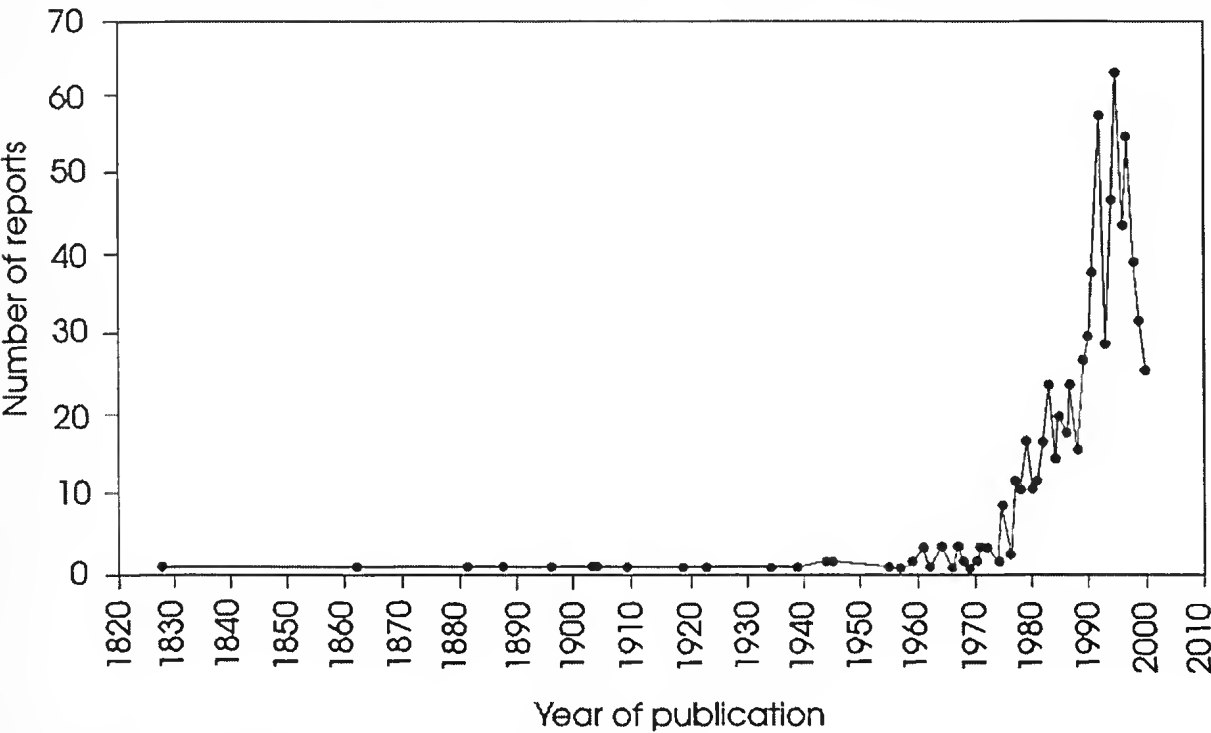
Figure 1. Reports captured during the project by year of publication

5. Maintaining a current listing of the authors of these documents

The maintenance of a contact list for any industry is a significant task. The database collated a range of contact details for reports. However, there has been no maintenance of the database since the end of the first phase of the project (June 2001), and as a consequence the information is already outdated. Therefore, the project has not met its objective of maintaining a current listing of the contacts.

A method for keeping the contact lists up to date is by registering visitors to the web site. The project recommended that registration should be free. Once a contact list was generated, it would be possible to automate an annual registration e-mail that included a hyperlink to the person's record within the database. Since the database employs relational structures, rather than update every single report, individuals would simply update a 'master' record and all reports with a link to this record would reflect any changes that the person has made. Of course, such development would attract a cost that would have to be borne at some point by the custodial organisation (currently CALM).

It should be noted that there are other alternative contact lists available to interested parties – such as the Environmental Consultants Association of Western Australia contact list, available on the WWW at http://www.eca.org.au/. Replicating the maintenance of a number of contact lists is not an ideal solution and it seems that it may be more efficient to remove this objective from further work on the project.

6. Becoming a one-stop reference point for all surveys undertaken in the Pilbara

Although listed as the final objective, this is perhaps the most important objective. Had the project managed to source and collate descriptive information for all identified reports, the database would have a much greater value. Additional reports listed in the references for these 589 reports would have added to the number of relevant reports for the Pilbara region.

While the project has not fulfilled all of the objectives that PIEC set for it, there is still value in the project. The fact that the project has captured information about the areas that have been surveyed in the Pilbara is of value. The project also enhanced the understanding of the issues associated with data management, data capture and data maintenance, and proved that a web-based deployment could be undertaken. One of the most encouraging results of the project is that a wide range of literature that would otherwise be closeted in private libraries (the 'grey' literature) is made publicly available.

Two major issues are of importance to the future of this project:

* quality – assessing the quality of biological surveys was not addressed during the project; and
* data capture requirements – who and how will the data be maintained.

Each of these future issues is discussed below.

Quality

The project originally had a requirement to rate the quality of the survey undertaken and documented in each report. As the organisation undertaking the work (Biota) was a private commercial organisation, a potential conflict of interest was identified early on in the project. It was seen as undesirable to have a commercial organisation develop a quality ranking system and subsequently rate a competitor's work, without some form of appeal or input from the authoring organisation. Professional societies such as the Ecological Society of Australia (ESA) acknowledge this hindrance to quality assurance in the biological/ecological consulting industry (ESA, n.d.). As a potential solution to this problem, the ESA advocates peer review as a means of quality control. A specific proposal for the WA environmental community is currently being prepared by Teale & Higgs (unpublished data).

The issue of devising both quantitative and qualitative assessment criteria in a stand-alone project was seen by PIEC as problematic. As studies such as Fraser *et al* (2003) have shown, there is no standard methodology for assessing the quality of surveys. While the quality of an environmental survey can to some extent be determined from quantitative assessment of the methodology used, other qualitative aspects need to be taken into account, such as the experience of the biologists performing the survey. Once a best practice standard can be agreed upon and set in place by the regulatory agencies, it is more likely that the quality of biological surveys can be adequately assessed.

Data capture requirements

Given that no data collection has occurred since May 2001, the database does not include any information from contemporary reports produced for the Pilbara since this time. Therefore, apart from the 589 reports that still need to be sourced and have descriptive information captured, there are potentially many additional reports that have not even been identified by this project. If the project was broadened in scope to include invertebrate surveys, which are often ignored in biological survey efforts (Bisevac & Majer 2002), then this is likely to include many more surveys.

From the experience of the first phase of the project, between 15 minutes and one hour is required to adequately collect descriptive information and enter it into a database for each report. The duration of data capture varies according to the length of the report being reviewed, but would average at 30 minutes per report. Therefore, between 400 and 650 person hours would be required to complete the data gathering for the Pilbara bioregion.

In addition to capturing the already identified but not assessed biological survey reports, the future of this project must consider the ongoing capture of newly produced reports. One option is to capture new reports on an annual cycle, as recommended by the final report of this project (Biota Environmental Sciences 2001b). If this occurs, it is estimated that approximately 30 to 40 reports per year would be produced for the Pilbara. From an initial analysis of the reports contained in the database, the majority of reports were published early in the calendar year (January – May). An annual update cycle in June would capture a large number of these reports within an acceptable timeframe. Additional time

would be required to update the Western Australian Herbarium database, which is in the order of 30 person hours per year.

The process of maintaining these data is not currently part of any existing business process but has been considered to instead be an annual commercial tender. It is well established in efficiency and performance literature that piecemeal approaches, such as annual tendering, can return little, if any, returns (*e.g.,* Rummler & Brache 1995). In order to avoid a piecemeal approach, it is suggested that existing, established business procedures are used (with modifications) to maintain this database. There are two business processes that appear to be ideal for capturing this information:

- The Environmental Impact Assessment and ongoing licensing processes undertaken by the Department of Environment (DOE)
- The Wildlife Licensing process undertaken by the CALM

Each is briefly discussed below.

The EIA and ongoing licensing processes

The EIA process relies upon biological survey reports to function. Organisations undertaking an EIA process produce reports, such as Public Environmental Reviews, Environmental Review and Management Plans and Consultative Environmental Reviews, that are provided to the EPA for assessment. Since the assessment officers must review these documents as part of the assessment, it is possible that this existing process could be modified to include data collection. This would involve the assessment officers at the DOE capturing descriptive information about the report, that is stored within an appropriately designed database.

In another process, Annual Environmental Reports are generated by organisations for the purposes of licensing. These reports provide environmental information in relation to their operations, which can include ongoing monitoring and other biological survey data. The DOE also reviews these reports, and the process could be modified in a similar manner to the EIA process.

The wildlife licensing process

The wildlife licensing process requires the submission of any reports relating to licences. When studies that include collection of animals are to be undertaken, a licence is required from CALM. This licence includes the condition that copies of any reports must be delivered to CALM within one month of the licence expiry. This is a second potential process for modification to include collection of descriptive information.

Wildlife licensing only requires reporting on fauna surveys under the *Wildlife Conservation Act 1950*. Flora licensing (under the CLM59 licence "Scientific or Other Prescribed Purposes Licence to take protected flora from Crown Land for non-commercial purposes") does not require specific reporting as it is a blanket licence for an individual for a period of 12 months. This licence requires lodgement of specimens to the Western Australian Herbarium. The wildlife licensing process in its current form will not capture biological survey data on non-threatened or protected fauna, or on general flora or vegetation surveys. Unlike the EIA process, it may

capture a range of academic research as licences are routinely issued for many of these studies. One of the issues that is raised with this process is that copies of reports or specimens are not provided to CALM as specified on the licence, and this is poorly enforced (S van Leeuwen, pers. comm.)

It is not probable that any change, no matter which processes are involved within either organisation, will be able to capture descriptive information about every single biological survey undertaken. Research or theses completed by research institutions such as universities, or reports commissioned by mining companies that are not as a result of the environmental legislative requirements are two examples of reports that will not be captured. However, by making changes to existing processes, such as the EIA or wildlife licensing processes, it may be possible to capture a significant proportion of the biological survey reports produced within Western Australia.

It may be that other organisations, such as the Western Australian Land Information System (WALIS), would be ideally suited to accept responsibility of this database and co-ordinate the efforts of other organisations. WALIS, who manage a range of descriptive databases, could also deliver a significant economy of scale, and can provide considerable expertise in managing this data, despite a relative lack of expertise in the biological sciences.

Given the fact that significant time has passed since any data collection has been undertaken, it is highly recommended that the project is thoroughly reviewed (using holistic models such as the Information Technology Interaction Model proposed by Silver *et al* 1995) in order to consider changes made to organisations, processes and any relevant projects before any further resources are committed to it. It is likely that there have been significant changes to the capabilities of the Western Australian environmental community, which may have ramifications to future phases of the project.

Conclusions

This project has raised important considerations for the practitioners of biological data management in Western Australia and future developers of similar or related systems should consider the issues of data quality and ongoing data capture. In particular, it highlights how an investment in technology, without an appropriate consideration of related business processes, cannot be entirely successful. However, as a case study for the management of biological data and information, it provides useful information. It has partially captured information about the types and extents of biological surveys in the Pilbara, and, should the project continue to further phases, would continue to capture and document this information.

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Drainage Evolution in the Lake Disappointment Catchment, Western Australia – a discussion

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Abstract

Lake Disappointment, one of the largest playa lakes in Western Australia, lies in an interior basin at the lowest point of a catchment 600 km E-W by 500 km N-S. A major tributary in the NW, Savory Creek, is still intermittently active but most other drainage channels are dry. Except for occasional rocky ranges the country is dominated by linear sand ridges which are vegetated with spiny grasses inedible to stock, and make access difficult. The country is therefore unoccupied. The sand ridges are thought to date from the last glacial maximum when climate was windy and dry. Drainage channels were formed much earlier under wetter conditions and have often been obscured by sand so that mapping must depend on contours, on valley-bottom calcrete deposits, salt lakes and pans. The catchment features a major palaeochannel, the Disappointment Palaeoriver, extending due south from the lake and receiving tributaries from both east and west. It is situated along the geological boundary between Proterozoic rocks of the Western Shield and Phanerozoic sedimentary rocks to the east. Lake Disappointment has no outlet nor any obvious sign of one. It must originally have reached the Percival Palaeoriver to the north and previous authors have favoured an outlet running north-east from the Lake and then north to Lake Winifred. It is suggested here that the Disappointment Palaeoriver continued to the NW to join Savory Creek, then passing north to join the Rudall River which would have been the lower course of a major river draining the whole Disappointment catchment. Disruption of drainage was presumably caused by tectonic movement, either slight uplift of the ridges to the north, sinking of a basin at the lake site, or both. A date of Miocene for this event is suggested.

Keywords: drainage evolution, Lake Disappointment, palaeoriver, playa,

Introduction

This paper continues a series on drainage evolution on the Western Shield (Beard 1998, 1999, 2000, 2002, 2003), and in particular continues to the north the study in Beard (2002) which the area adjoins. The work involves an analysis of the geological, topographical and biological features of the catchment and from historical records working out the course taken by waterways in the past and how these have changed to the present day. Lake Disappointment lies at approximately 23° 30'S, 122° 45'E and is one of the largest playa lakes in Western Australia measuring 45 km north to south and averaging about 25 km east to west, thus covering more than 1000 km². It is situated in a basin at the lowest point of an extensive catchment 600 km east to west and 500 km north to south, of which the southern section was partly dealt with in Beard (2002). At the present time most drainage channels in the catchment are dry or flow briefly after rain, having been formed in more pluvial periods in the past. The lake lies in the phytogeographic region known as the Little Sandy Desert (Beard 1969), bounded by the Great Sandy Desert on the north, the Gibson Desert on the east and the Pilbara region on the west. The catchment itself falls partly in the Little Sandy Desert region and partly in the Gibson Desert. Figures 1 and 2 show it in its phytogeographic and geological settings. Owing to the remoteness of the area the lake was not found and named until 1897. Ernest Giles on his west to east desert crossing of 1878 passed to the south

on lat. 24° and did not sight it, while the Calvert Exploring Expedition of 1896 travelled from south to north on the west side of the lake, without sighting it. The lake is not mentioned in either account of this expedition (Hill 1905, Steele 1978). It was left to Frank Hann in the course of an exploring/prospecting expedition travelling east from Nullagine to sight and name the lake on 20 April 1897. Hann had travelled from Nullagine across the Davis River to the Coolbro Creek, then to the southeast following and naming the Broadhurst Range, crossing the upper Rudall River and the Cotton Creek as far as the Harbutt Range where he turned south to the Mckay Range. Here to the southward he sighted a large lake ten miles distant, and they made their way to it next day, but "found it was all white salt....it is the largest thing in lakes I ever saw... I shall call the lake Lake Disappointment as I was disappointed in not finding water in it" (from Frank Hann's diary quoted by Donaldson & Elliott, 1998).

The country surrounding the lake is uninhabited and very remote, largely because it is covered for the most part by linear sand ridges through which occasional rocky ranges protrude. The Canning Stock Route, used at one time for driving stock south from the Kimberley and today by venturesome tourists in 4-wheel drive vehicles, passes from the Durba Hills round the west and north of the Lake, and a similar east-west driveable track, the Talawana track, passes on the north of the Lake, joining tracks in the Gibson Desert to the outside world at Talawana Station. The Aboriginal population reported by the 19th century explorers later gradually withdrew to settlements on the fringes of the desert, mainly to the
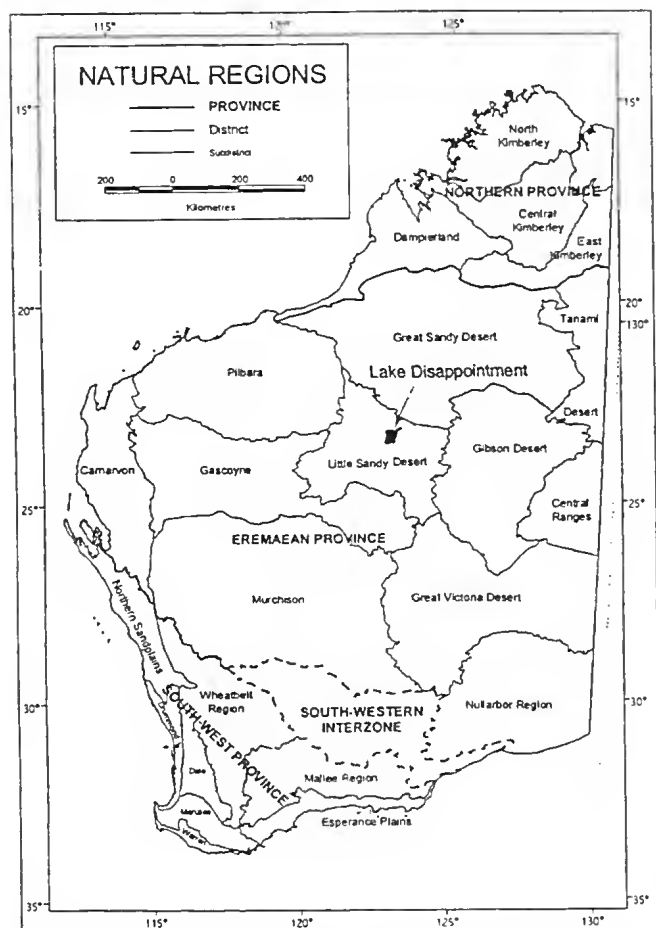
Figure 1. Lake Disappointment in its phytogeographical setting. Natural Regions after Beard & Sprenger (1964).

Figure 2. Lake Disappointment in its geological setting. From figure in Beard (1998) based on Figures. 3.1 and 4.1 of Anon (1990).

Jigalong community (see map, on Robertson sheet).The country has not been subsequently developed for pastoral use largely because it is covered by "hard spinifex", spiny species of *Triodia* which are inedible by stock. The general cover of sand ridges, also, makes access difficult.

It is difficult to map precisely the boundaries of the catchment because much of the topography is so obscured by sand ridges that drainage lines and watersheds are hard to trace. The catchment features a main north-south axis, formed by the Disappointment Palaeoriver, extending south from the lake for 300 km, which receives palaeotributaries from both east and west (Fig. 3). The principal of these are the Keene Palaeoriver on the east and the Ilgarari Palaeoriver (Williams 1995) on the west, both over 300 km long. In the northern part of the region and flowing directly into the lake from the north-west, there is a well-marked intermittent stream, Savory Creek. The lake itself has no present outlet nor any readily discernible former outlet, so that it seems likely that it has been formed as a result of some tectonic movement, either sinking of the lake basin or uplift of ridges to the north, or both of these.

Methods

The southern and eastern parts of the catchment had been mapped and studied as part of a similar paper on

drainage evolution in the Gibson and Great Victoria Deserts (Beard 2002), and this paper extends the study to the north and west. The latest series of 1:250,000 topographic maps was examined, drainage lines and watersheds were marked and transferred to compilation sheets at 1:1,000,000. Since in sandhill country it is often difficult to distinguish such features accurately, reference was also made to the 1:250,000 Geological Survey reports which normally include a "physiographic diagram". These are not standard but in various ways indicate physical features and drainage lines. Where no actual creeks are shown, drainage lines can be inferred from valley-bottom calcrete deposits. The map in Figure 3 is the result of this compilation. In addition, a request was addressed to the Water and Rivers Commission for any available borehole data from within 100 km radius of Lake Disappointment, and figures were supplied from 28 bores and/or wells within this area, all on the west and north sides of the lake. Unfortunately, the remoteness of this area and the lack of mineral prospects meant that all had been sunk to relatively shallow depths in the quest for water alone, and in particular there were no bores in the bed of the lake. Of the 28 bores/wells, four had no depths recorded, and 11 were pre-existing wells of the Canning Stock Route between bore/well numbers 15 and 26. Some of these had perhaps been deepened, and reached depths of 16 m. Of the rest, only five went to depths of more than 30 m, with a maximum of 65m. Average depth of all bores/wells was 19.20 m. Drilling was through surface sand into sandstone or calcrete. A

Figure 3. The Lake Disappointment Drainage System with the entire catchment outlined in grey.

complete study of Lake Disappointment and the history of its formation would require a drilling programme in the lake bed to determine the depth, age and nature of buried sediments, and this is not at present available.

Features of the Area

The name Little Sandy Desert was proposed by Beard (1969) for "a sector of the desert which appears to have been nameless hitherto and is chosen to reflect the fact that its character is much the same as that of the Great Sandy Desert from which it is partly isolated by a chain of hills and ranges". Both of these Deserts were described as "an impenetrable waste of sandhills"(ibid.), but the Little Sandy differs in being underlain by Proterozoic rocks instead of Tertiary sediments. This basement forms rounded hills and mountains emerging from a sea of parallel sandhills each of which may be as much as 160 km long and spaced at six to the kilometre. The bed of Lake Disappointment is at 325–330 m above sea level and the catchment slopes down towards it from all sides from a maximum height at Mt. Methwin of 913m.

Climate

This is a desert area, in which high day-time summer temperatures of 45°or more can be experienced as well as night-time winter temperatures below freezing. Rainfall is about 200 mm per annum and not so low as to create areas without plant cover. Rain can be received both from the relics of tropical cyclones which have come in from the sea off the north-west coast, or from an extension of the late summer-autumn rainfall regime of the Murchison region to the south. In both cases rainfall is very erratic, and long droughts are known to occur.

Vegetation

The vegetation of the area has been mapped at a scale of 1:1,000,000 by Beard (1974,1975) with explanatory memoirs, and there are sections on the Little Sandy Desert in Beard (1969, 1990). Broadly, the whole country is covered by Hummock Grassland formed by species of *Triodia*, spiny grasses growing in isolated clumps, with scattered shrubs and small trees. Hills are generally very rocky so that vegetation is sparse. There are small trees about 4.5 m of the mulga *Acacia aneura* with shrubs of *Grevillea, Hakea* and *Thryptomene* but there are also areas of hummock grassland consisting of both *Triodia basedowii* and *T .melvillei*. Scattered larger trees of *Eucalyptus camaldulensis* occur here and there. The gullies have *E. microtheca* and *Callitris glaucophylla*. The sandplains carry spinifex country of *Triodia basedowii* with numerous tall shrubs, principally of *Hakea suberea* and *Acacia* spp. with *Hakea rhombale*. On sand ridges the general cover is of *Triodia schinzii* with the ericoid shrub *Thryptomene maisonneuvii* sharing dominance on the flanks of the dunes. The desert bloodwood *Eucalyptus chippendalei* occurs as scattered trees along the dune crests with shrubs of *Acacia ligulata* and *Grevillea stenobotrya*. Groves of the desert oak, *Casuarina decaisneana*, may occur in depressions between the sandhills.

Geology

The geological setting of the Lake Disappointment catchment is shown in Figure 2. In simple terms, the geology of Western Australia (excluding the Kimberley) can be interpreted as a central massif of Proterozoic and Archaean age, bordered on the north, west and east by sedimentary basins. More detailed mapping shows the Shield divided into two cratons, the Pilbara Craton in the north and the much larger Yilgarn Craton in the south, divided by a belt known generally as the Capricorn Orogen which can be further subdivided into Proterozoic basins and orogens. The Little Sandy Desert which largely corresponds to the Lake Disappointment catchment is situated at the north-west corner of the Shield, and is underlain geologically by the Savory (geological) Basin (Williams 1990) and the Paterson Orogen (Williams & Myers 1990), both containing Late Proterozoic rocks. These are bounded on the north by the Canning Basin and on the east by the Officer Basin, both containing Phanerozoic sediments.

The Savory Basin mainly comprises gently east-dipping medium to coarse-grained sandstone and pebbly conglomerate. For the most part bedrock is poorly exposed and limited to marginal ranges such as the Robertson Range or to scattered rocky hills such as the Poisonbush Range. In general the topography is monotonous and obscured by linear sand ridges. The surface sand which covers most of the Little Sandy Desert in this way is considered to have been derived from the underlying sandstone. A very detailed description of the sand dune formations in the area was included by Williams (1995) in the geological survey report on the map sheet Bullen. It is thought that the dunes were formed by wind action during the last glacial maximum at 13–25 Ka, most likely during the intense phase at 15–18 Ka.

The Paterson Orogen consists of a belt of metamorphic and igneous rocks with a long and complex history of multiple deformation and metamorphism (Williams & Myers 1990) which form a series of low rocky ranges trending NW to SE. These will be found on the map in Figure 3 as the Throssel and Fingoon Ranges, the Connaught Hills and the Harbutt Range, rising to heights of 450 to 550 m, with a relief of 100–200 m. The age of these rocks is estimated as Proterozoic, and rather older than those in the Savory Basin. The geological history shows that this topography is of long standing, since there are former valleys filled locally with Permian glacial sediments. One can envisage that during the ice-age conditions of the Sakmarian stage of the Permian there were glaciers flowing off the Western Shield to the Canning Basin, where Permian sediments are widely distributed. While interesting, this history has no bearing on modern conditions.

The Disappointment Palaeoriver

This portion of the Lake Disappointment system has been described in a previous paper (Beard 2002) from which some of the conclusions are repeated here. The channel leading north into the lake was named the Disapointment Palaeoriver by van de Graaf *et al.* (1977) who connected it to Lakes Carnegie and Wells. Beard's (1973) map had shown this drainage, south of the confluence with the Keene Palaeoriver which comes in from the north-east, as flowing originally to the south and finding an outlet to Lake Throssel (outside Figure 3 to the south-east). Van de Graaf *et al.* (1977) agreed with this as the original alignment but considered that the

system north of Lake Wells had been reversed to the north at a later stage. A notable feature of this drainage line is that it is situated along the geological boundary between the Archaean and Proterozoic rocks of the Western Shield and the Phanerozoic rocks of the sedimentary basins to the east. Beard (2002) suggested that this drainage line was originally formed after the end of an Early Cretaceous transgression by rivers which continued to discharge eastward off the Western Shield and were impounded at the break of slope at the former shore line. It is probable that flow took place partly to the north and partly to the south.

Examination of the maps shows a valley floored here and there by salt lakes and pans extending south from Lake Disappointment. From the lake bed the valley trends uphill to the 400 m contour in 100 km (0.75 m km⁻¹) and then at a lower grade to Lake Burnside at 425 m in another 90 km (0.28 m km⁻¹) – (Fig. 4). South of lake Burnside the alignment continues uphill to Lake Bedford at 443 m and beyond to a source on high ground at about 480 m. Beard's evidence from the mapping showed clearly that this valley represented the Disapppointment Palaeoriver, that the tributary Keene River joined it, but that there is not and has never been any outflow from Lake Carnegie to Lake Disappointment. Lake Carnegie was shown to have discharged to the south via Lake Wells. On the other hand the south-westerly alignment of the Keene Palaeoriver suggests that it originally had an outlet to the south and Beard (2002) suggested that it had originally found its way into Lake Carnegie at its north-western end, but was later diverted by tectonic movement northward into Lake Disappointment.

The drop at the north end of the palaeoriver into Lake Disappointment is much steeper than the grade higher up in the catchment, so much so as to suggest a downwarp at the site of the lake. However the opposite may also have been the case, i.e., uplift of the upper part of the catchment. Beard's (2002) study of the geomorphology of the Gibson and Great Victoria Deserts showed that these had been subject to repeated tectonic movements from the early Cretaceous onward with alternating periods of uplift and depression coinciding with such movements in the Eucla Basin. These movements apparently weakened towards the north and while the southern part of the Disappointment Palaeoriver was evidently included, the northern part and the Lake itself were not. A profile of the Disappointment Palaeoriver is included here based on the 2002 paper (Fig. 4).

On the west side a substantial palaeoriver came in to join the Disappointment Palaeoriver, but downstream of the Keene river, and hence not affected by the same tectonic movement. This is the Ilgarari Palaeoriver, usefully named, described and mapped by Williams (1995) in the revised edition of the geological survey of the map Buller. This begins as a combination of small creeks rising like Savory Creek in the Central Watershed of the Western Shield, and terminating in salt lakes on reaching sandhill country. These include the Ilgarari Creek itself which penetrates as far as Terminal Lake and the Nanyerinni and 477 Creeks which empty into the Beyondie-Ten Mile Lake system. Strings of disconnected salt lakes and patches of valley calcrete connect and continue these drainages to the east eventually to join the Disappointment Palaeoriver.
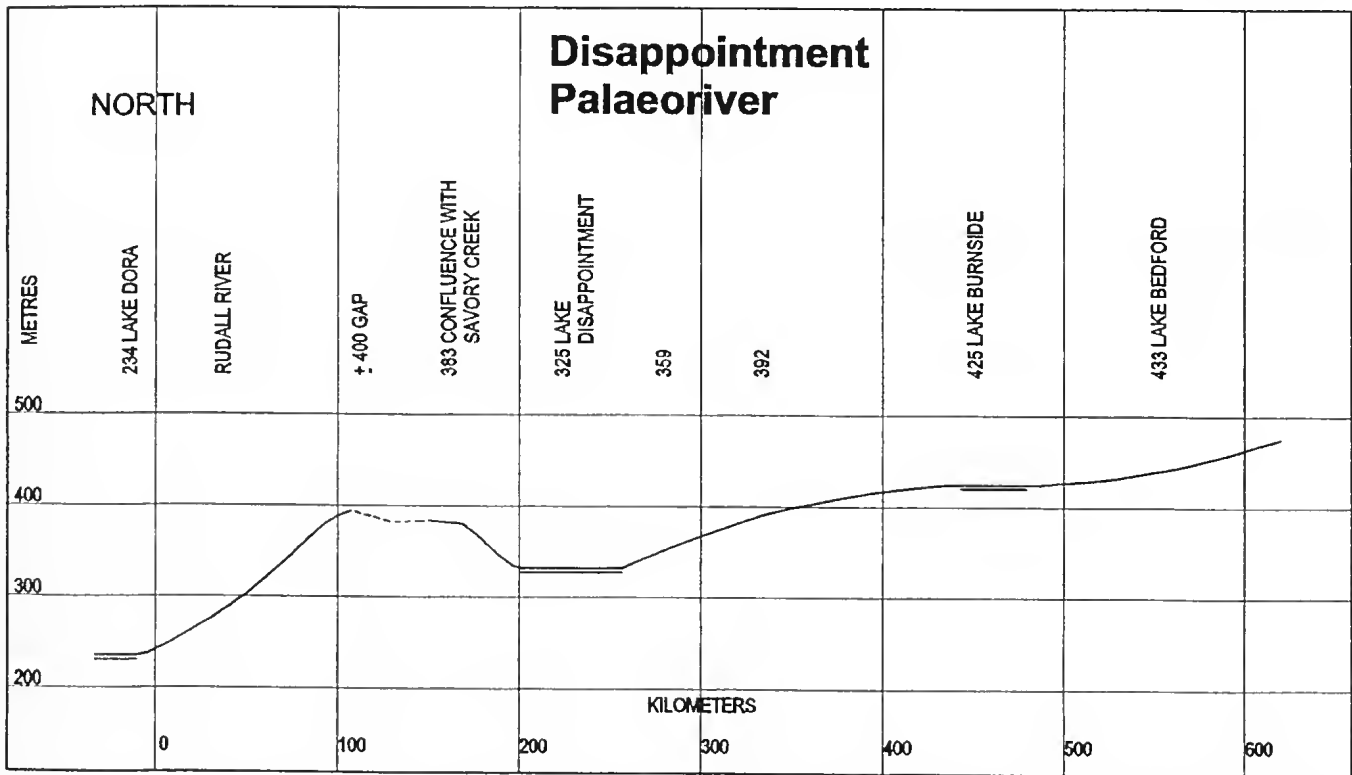
Figure 4. Profile of the Lake Disappointment Palaeoriver based on Fig.5A in Beard (2002) extended further to the north to include line of suggested former outlet joining the lake to the Percival Drainage System at Lake Dora, now obstructed by tectonic movement.

Savory Creek

Savory Creek has features which differ from other tributaries in this system and deserves special mention. It is unique for the area in being a still active river. The origin of the name is given in a note in Fieldbook 43 of A.W.Canning in 1904 when he was on a reconnaissance for the later Canning Stock Route, saying that it was named after a Mr.Savory who held a pastoral lease in the area. From its source to the lake, Savory Creek is 320 km in length and flows mostly through sandhill country. It rises in the Central Watershed of the Western Shield at a spot height of 646 m and after quickly levelling off at about 600 m it flows for the next 260 km at a steady grade of about 1 m per km, heading first east and then north-east. Along this stretch it has a well-defined branching channel incised to a depth of 20 m in places, and containing thick vegetation and pools of relatively fresh water. On reaching what is evidently a flat area at a spot height of 383 m where flood-out conditions prevail, the Creek turns to the east and divides into several widely separated saline channels up to 10 m deep, which support little vegetation apart from samphire communities (Williams & Williams 1980). After 20 km these channels unite and reach Lake Disappointment in another 30 km. This behaviour suggests strongly that Savory Creek at one time continued to flow to the north through a gap in the ranges, round the western end of the McKay Range to reach the Rudall River. Calcrete deposits are evidence of former drainage lines along this route but at the present time the slopes head south-east towards Lake Disappointment. This calcrete is shown as a surface deposit in the geological survey (Bagas *et al.* 2000) and is not in inverted relief which would be evidence of greater age. Intermittent drainage comes in to Savory Creek from the north at the point where it takes its turn to the east. This comes from a small lake some 10 km to the north, and above this there are calcrete deposits probably representing palaeochannels which head to the southeast from the direction of the Poisonbush Range. However these could have been formerly picked up by Savory Creek on its way to the Rudall River and later reversed by tectonic movement.

In the geological survey report (Williams & Williams 1980) it is suggested that the salt lakes are migrating to the east. Fresh bedrock occurs on the eastern side of Lake Disappointment whereas extensive kopi and sand-buried lake deposits fringe the western margin. Low breakaways also occur on the western side of the McFadden Ranges. This behaviour is contrary to that observed in the southern part of the State.

Outlets from Lake Disappointment

Figure 5 has been designed to show the area north of the lake in more detail. Previous authors (Williams & Williams 1980, Crowe & Chin 1979) have shown the lake with an outlet to the Percival Palaeoriver in the Canning Basin, connecting at Lake Winifred south of Lake Auld, which has an elevation of 261–263m. These are about 65 m lower than Lake Disappointment but there is no obvious palaeochannel between the two. A line of lakes and pans leads to the east from the north-east corner of Lake Disappointment, but without any indication of an outlet to the north to Lake Winifred. In any case a col 30 m higher than the lake stands in the way of this outlet. It

is equally possible that the line of lakes and pans represents former drainage of tributaries from the east into the lake. It seems logical to conclude that in the distant past the lake or the river which preceded it must have had an outlet to the Percival System at some point which could have been as described above or via Savory Creek to the Rudall River. The Percival has in the past been the major drainage outlet for this whole area. It seems less likely that the lake basin has existed as an interior basin since a geologically early date and this question cannot be resolved until borehole data may become available to reveal the depth and dates of accumulated sediments.

The 1999 geological map of Western Australia (Anon 1999) clearly shows the Percival Palaeoriver, named as such, by showing lakes and channels in blue and by mapping of alluvial bottom-land deposits. It rises far to the east at Wilson Cliffs on high ground near the State boundary at lat. 22° 00'S, long. 127° 30'E, and heads to the west for 300 km, then turning to the south along the length of Lake Auld for 140 km., with heights of 261–263m. Turning then to the SW through the smaller Lakes George and Winifred it swings to the NW along Lake Blanche (254m) to Lake Dora (234–229m), a distance of 90 km. From Lake Dora in a NW direction the channel heads for Lake Waukarlykarly (233m), 140 km away. There are no more lakes and pans but the alignment is shown as a valley by the contours, floored by calcrete deposits. It passes north of Telfer Mining centre between the Malli Hills 331m and Kaliranu Hill 334m. There is very little fall along this stretch. The channel leaves Lake Waukarlykarly in a westerly direction for 40 km, then bears to the NW for 100 km, where it unites with the Oakover River north of the Isabella Range. Although thus reduced to the status of a tributary to the Oakover and de Grey active rivers of the Pilbara, the Percival is one of the most substantial drainage lines in the State with a length of 800 km.

Discussion

It seems clear that Lake Disappointment was originally formed by being impounded when outlets were obstructed by various means, possibly obstruction by dunes, deflation or tectonic movement. This last seems the most probable. Such movements on the fringes of the Western Shield have been reported elsewhere (Beard 1999,2000,2003). In this case the shape and situation of the lake suggest the sinking of a basin which received flow from the Disappointment Palaeoriver when it was active, and accumulated sediment from that source. The sinking of this basin evidently affected Savory Creek also, diverting the flow into the lake. It seems likely that drainage from the east was drawn into the lake in the same way. It seems likely also that tectonic movement was not confined to the sinking of the basin, but involved some uplift of the ranges in the Paterson Orogen. These are arranged north-west to south-east along the flank of the Western Shield but there is only one substantial river, the Rudall River, draining them towards the Percival system. Why is this? There seems to be no reason why the Connaught Hills should have given rise to such a stream when the other ranges have not. The Rudall River is aligned with Savory Creek and it is suggested here
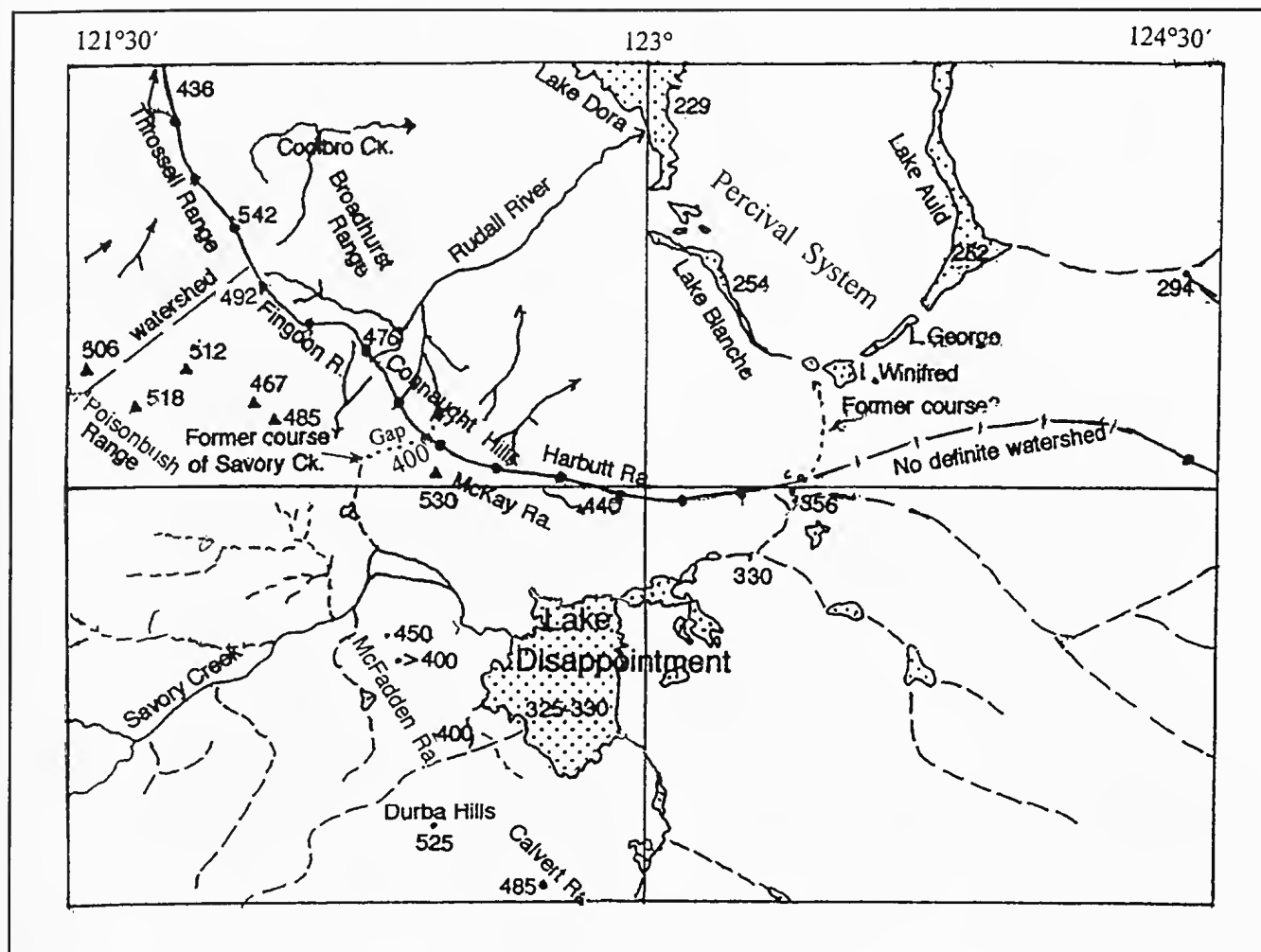
Figure 5. Larger scale map of the area between the Disappointment and Percival Systems where former outlets were located.

that Savory formerly continued to the north, so that the Rudall is the remnant of its lower course. The highest point today on the probable course joining the two, where "Gap" is marked on the map in Figures 3 & 5 is at about 400 m. If Savory Creek continued to this spot at the same grade as it maintains for 100 km upstream from where the 400 m contour is marked on the map, the height would be about 350 m. It is therefore concluded that an uplift of about 50 m occurred, reversing the upper Savory into Lake Disappointment. It seems probable that the same thing happened north-east of Lake Disappointment where drainage flowing to the north from the Gibson Desert plateau to join the Percival system below Lake Winifred was diverted into the lake. While this seems to show that there has been tectonic uplift affecting the Connaught Hills and associated ranges, there would appear also to have been down-warping of the lake area, because the point where Savory Creek turns to the east towards the lake is some 60 m higher than the lake surface, and the actual lake bed, filled with sediment, is lower still. On the other hand, if we look at the profile of the Disappointment Palaeoriver in Figure 4 which extends the original diagram in Beard (2002) to include the suggested outlet to the Rudall River, and draw a straight line from Lake Burnside to Lake Dora, it is found that the line passes through the north

end of the Lake. This suggests that there has been relatively little subsidence of the lake bed compared with the uplift of the Connaught Hills and other ranges, which would be of the order of 100 m.

Some evidence for the dating of this event can be derived from the fact that the rivers concerned were already losing their erosive capacity. If a tectonic barrier is raised across a major drainage system as the Savory-Disappointment system must have been early in the Tertiary, then the river can keep pace with uplift and carve an antecedent gorge. There is no sign of this, so that a later date of Miocene is suggested.

Conclusions

For final conclusions to be drawn about the development of this area it would be necessary to have borehole data from the bed of the Lake to show the thickness and nature of sediments and their age, and these are not at present available. It is tentatively concluded that the Rudall River was originally the lower course of Savory Creek which continued to flow to the north through the Connaught Hills but has been diverted into Lake Disappointment by a combination probably of uplift of the ranges in the Paterson Orogen and of sinking

of a basin on the site of the Lake. Prior to that event the Disappointment Palaeoriver flowed to the north-west across the present site of the lake to unite with Savory Creek and Rudall. While not conclusive, the data do appear to show that tectonic movement occurred. It is impossible at present to date this event accurately but a date of Miocene is suggested.

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Temporal variation in subtidal macroalgal assemblages at Black Island, Recherche Archipelago

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Abstract

Temporal patterns in subtidal macroalgal diversity have not been described for much of temperate, southern Australia. To characterize temporal variation in species diversity, subtidal macroalgal assemblages were compared between austral spring and autumn collections from Black Island, Western Australia. Macroalgae (> 1 cm in length) from 0.25 m^2 quadrats were harvested from the south-eastern and southern sides of the island in depths < 10 m and 10–20 m in October 2002 and 2003 and April 2003 and 2004. Macroalgae were sorted, wet-weighed, and identified. A three-way analysis of variance tested for differences in total biomass, and density of thalli in the canopy with time, site, and depth. Analysis of similarity was used to test for differences in macroalgal assemblages among sampling times. Key environmental variables for the area were compiled from previous reports. A total of 254 species of macroalgae were recorded, consisting of canopy, understory, and epiphytic species. Average total biomass was not significantly different among sampling times. Density of thalli per 0.25 m^2 was greater and more variable in depths < 10 m than in depths 10–20 m. Macroalgal assemblages differed significantly among sampling times (Clarke's R values > 0.5, P = 0.001), and between samples collected from the same season but in different years. Each species was present, on average, in only 15% of the sampled quadrats. Chlorophyll *a*, seawater temperature, and salinity estimates did not vary much throughout the year with a range of 0.6 mg m^{-3} for chlorophyll *a*, 2.3 °C for seawater temperature, and 0.2 ppt for salinity. Year-round exposure to wind and wave energy from Southern Ocean gales and storms may drive the high species turnover and variability in density of thalli in depths < 10 m.

Keywords: Australia, exposure, macroalgae, seasonality, subtidal.

Introduction

Changes in composition and relative abundance of subtidal macroalgae have been correlated to seasonal patterns in temperate, sub-tropical and tropical habitats. For example in central California, temperate *Macrocystis* kelp forests have a predictable seasonal pattern: a minimum surface kelp canopy during stormy winter months and a maximum in summer and autumn months; recruitment of understory annual species greatest in spring and summer; and perennial species present throughout the year, though during winter only holdfasts may be present (Reed & Foster 1984, Breda & Foster 1985). In temperate southern Korean reefs, species richness is greatest in winter and cover is greatest in spring (Kim *et al.* 1998). In sub-tropical Baja California Sur, Mexico, algal biomass is lowest in spring with a maximum in summer when seawater temperatures are highest (Nunez-Lopez & Valdez 1998). In tropical coral reef habitats in Colombia, increases in the biomass of algal turfs were correlated to seasonal rains in April-June and October-December, and increases in the abundance of *Dictyota* spp. were linked to periods of upwelling in August and February (Diaz-Pullido & Garzon-Ferreira 2002).

By comparison, seasonal variations in subtidal macroalgal assemblages have not been described along much of the southern coast of Western Australia due, in part, to the remoteness of field sites and rough subtidal conditions. In Tasmania, growth in subtidal macroalgae was reported in spring-summer and winter-spring with similar densities of canopy taxa throughout the year (Edgar 1983). In South Australia, Shepherd and Womersley (1970) observed that more common species were present throughout the year with growth evident from winter to early summer and algal thalli were denuded by midsummer. Inadequate data of smaller species precluded any conclusions regarding seasonal abundances (Shepherd & Womersley 1970). Building upon the findings of Shepherd and Womersley (1970) and Edgar (1983), the present study describes temporal variation in subtidal macroalgal assemblages at Black Island in the Recherche Archipelago and relates findings to local oceanographic variables. Standing crop (biomass), density of thalli in the canopy, and macroalgal diversity (species richness and relative abundance) were compared among four sampling times in the austral spring (October 2002 and 2003) and autumn (April 2003 and 2004) at two sites and depth strata. Fertile specimens were also reported.

Methods

Study site

Black Island (33° 55 S, 122° 00 E) is located in Esperance Bay, Western Australia, and is part of the

Recherche Archipelago, a collection of over 100 islands that spans 250 km. Typical of the islands in the archipelago, Black Island is granitic with subtidal reefs consisting of gently-sloping platforms and boulder fields that extend to depths of 30 m. The southern side of the island is relatively exposed to south-westerly swell rolling in from the Southern Ocean. The south-eastern side of the island is relatively sheltered from ocean swell. Subtidal macroalgal assemblages consist of a multi-specific, fucalean canopy that overlays an understory (species < 30 cm in length) with a few dominant taxa (< 5 genera) and a greater number (> 150 species) of relatively rare species (Goldberg & Kendrick 2004). The macroalgal assemblage at Black Island is typical of islands in the Recherche Archipelago with a canopy dominated by Fucalean species on the wave-sheltered side of the island, *Ecklonia radiata* and *Scytothalia dorycarpa* on the wave-exposed side of the island, and species-rich understory assemblage (Goldberg & Kendrick 2004). In addition, environmental variables collected in Esperance Bay would be relevant to any temporal variability observed in algal species diversity at Black Island. Urchins are uncommon and herbivorous fish have not been observed to diminish algal biomass in the Recherche Archipelago (Fowler-Walker & Connell 2002, personal observation in 2002 and 2003).

Description of seasonal variation in oceanographic parameters

Seasonal estimates of oceanographic parameters (seasonal chlorophyll *a*, sea surface temperature, wind speed, salinity, and wave height estimates) were compiled from previous and ongoing studies. Chlorophyll *a* estimates in Esperance Bay were taken from van Hazel *et al.* (2001). Sea surface temperatures (° Celsius) were provided by A. Pearce, CSIRO (unpubl. data, 26 October 2004). Data were collected by a StowAway Tidbit Temperature Logger that was deployed at a depth of 1.5 m and attached to a jetty piling at Woody Island, 3 km south of Black Island. Mean monthly sea surface temperatures were averaged over each season, 2001–2004: summer (Dec-Feb), autumn (Mar-May), winter (Jun-Aug), and spring (Sept-Nov). Additional temperature data were included from measurements recorded in Esperance (33° 51 S, 121° 54 E) in 1998 and provided by the Australian Oceanographic Data Centre (AODC 2004). Seasonal wind speeds (km hr^{-1}) from Esperance were supplied by the

Western Australia Office of the Bureau of Meteorology (Climate and Consultancy Section 2004). Salinity data and wave height data were compiled from archived information. Salinity data (ppt) for Esperance waters were provided by the AODC. Mean salinity per month was averaged per season. Significant wave height data (m) were collected from Magistrates Rocks, located within Esperance Bay from March 1982 to February 1983 (van Hazel *et al.* 2001).

Oceanographic estimates were similar throughout the year. In 2000, chlorophyll *a* concentrations were slightly greater (1.0 mg m^{-3}) in autumn than in spring (0.4 mg m^{-3}) (van Hazel *et al.* 2001). Between 2001 and 2004, mean seasonal sea surface temperatures differed by 2.3 °C with coldest temperatures occurring in spring (16.3 °C) and warmest temperatures in summer and autumn (19.0 °C; Table 1). Salinity was 0.2 ppt greater in summer and autumn compared to winter and spring (Table 1). Wave heights of 1 m were common, and waves > 2 m occurred 20–30% of the time throughout the years 1982 and 1983 (Table 1). Regardless of season, wind direction was variable throughout the year and wind speeds > 10 km hr^{-1} occurred > 57% of the time (Table 1).

Sampling methods

At Black Island, subtidal macroalgal assemblages were sampled in austral spring and autumn. Austral spring samples were collected in October 2002 and 2003, and autumn samples were collected in April 2003 and 2004. Macroalgae were collected in spring to sample species diversity following winter storms, and in autumn to sample species diversity following summer growth periods (Womersley & Shepherd 1970).

To test if temporal variation in macroalgal assemblages differed spatially along Black Island, two sites were sampled. These sites differed with exposure to wave energy. The southern site (33° 55.417 S, 121° 59.562 E) was located off a point and faced south-westerly swells. The south-eastern site (33° 55.188 S, 122° 00.003 E) was located within a narrow embayment protected from south-westerly swells.

Two depth strata were sampled because subtidal macroalgal assemblages differed between depths < 10 m and depths 10–20 m in a previous study. Goldberg and Kendrick (2004) documented an assemblage dominated by canopy taxa in depths < 10 m, and a mixed

Table 1

Oceanographic parameters measured in the Recherche Archipelago.

Parameter	Summer	Autumn	Winter	Spring
Sea surface temperature (mean °C ± se)				
a. May 2001 to Jan 2004, excluding Mar-May 2003 (A. Pearce, CSIRO)	a. 18.7 ± 0.18	a. 19.0	a. 17.2 ± 0.26	a. 16.3 ± 0.17
b. 1998 (AODC 2004)	b. 19.3	b. 19.3	b. 17.3	b. 16.5
Salinity (mean ppt ± se), Jan to Dec 1998 (AODC 2004)	35.9 ± 0.09	35.9 ± 0.03	35.7 ± 0.03	35.7 ± 0.03
Percent occurrence of significant wave height > 2 m March 1982–February 1983 (van Hazel *et al.* 2001)	20%	25%	30%	20%
a. Predominant wind direction Years 1995 and 2000 (van Hazel *et al.* 2001)	a. East/Southeast	a. East/Southeast, North/Northwest	a. Northwest	a. No dominant wind direction
b. Approximate percent occurrence of wind speed > 20 km hr^{-1}, January 2002–May 2004 (Climate and Consultancy Section 2004)	b. > 73%	b. > 57%	b. > 67%	b. > 74%

assemblage of canopy and understory taxa in depths 10–20 m at Black Island and other islands in the Recherche Archipelago. At each site, 0.25 m²-quadrats were placed randomly in depths < 10 m and 10–20 m (n = 6 per depth stratum). In each quadrat, macroscopic algae (> 1 cm long) were collected by hand and with a paint scraper. Macroalgae were sorted, wet-weighed, and fertile material was noted. Species identifications were made using Womersley (1984, 1987, 1994, 1996, 1998, 2003) and Huisman (2000). *Sargassum* species that were vegetative were identified to subgenus.

Data analysis

A three-way ANOVA was used to test for differences in average biomass and density of thalli in the canopy (fixed factors: time: n = 4, site: n = 2, and depth: n = 2). Data were square-root (X + 0.5) transformed to satisfy assumptions of equal variances and normality (Zar 1984).

To test for differences among the macroalgal assemblages with time, multivariate analyses were performed with biomass data. Data were fourth-root transformed to minimize ranges of biomass estimates (Clarke & Gorley 2001). From a Bray-Curtis similarity matrix (Bray & Curtis 1957), a one-way analysis of similarity (ANOSIM; PRIMER ver. 6 software, Plymouth) was used to test for the significance of assemblage differences among sampling times. ANOSIM calculates a Clarke's R test statistic that typically ranges between zero and one. Assemblages are considered to be relatively similar the closer the value is to zero (Clarke 1993). Differences in assemblages among sampling times were tested with a one-way ANOSIM within each depth-site combination. Separate tests were conducted because assemblages were significantly different between depths

and sites (Clarke's R_{depth} = 0.66, P = 0.001; and Clarke's R_{site} = 0.52, P = 0.001).

Results

A total of 254 species of macroalgae were recorded. Total species richness per sampling event showed no consistent difference between autumn and spring samples (Table 2). Species richness was greatest in spring 2003, irrespective of depth or site. At the southern site, average species richness per sampling time (± se) was similar between depths < 10 m and 10–20 (42 ± 5 species per sampling time and 43 ± 5 species per sampling time, respectively). At the south-eastern site, average species richness (± se) was lower in depths < 10 m than in depths 10–20 m (36 ± 5 species per sampling time and 55 ± 6 species per sampling time, respectively; Table 2). Average species richness per 0.25 m² ranged between 10 and 27 species.

Average total biomass per 0.25 m² was not significantly different among sampling times but the interaction term "depth x site" was significant (Table 3, Fig 1). Average total biomass was two-fold greater at the southern site than south-eastern site in depths 10–20 m (Fig 1). Per sampling time, 67% of the species contributed < 5 g per 0.25 m², regardless of depth or site. These species were primarily from the understory assemblage.

Table 2

Total species richness per sampling event. n = 6 per sampling event, site, and depth stratum.

Sampling Event	Southern site		South-eastern site	
	< 10 m	10–20 m	< 10 m	10–20 m
Spring 2002	36	38	25	38
Autumn 2003	45	32	34	61
Spring 2003	54	53	49	62
Autumn 2004	33	49	37	58
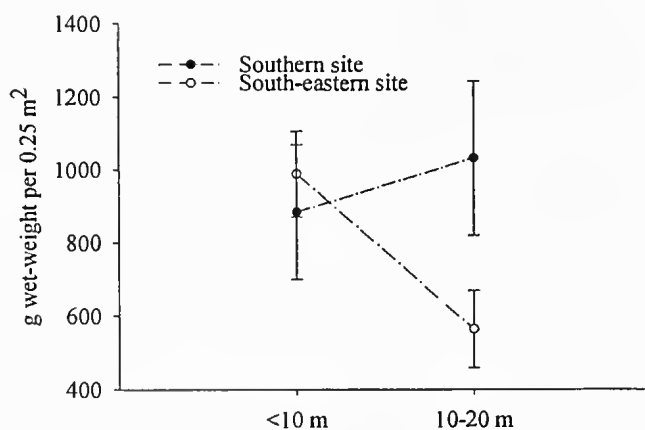
Figure 1. Illustration of "depth x site" interaction term for total macroalgal biomass per 0.25 m² (mean ± se) at Black Island. n = 6 per site and depth stratum combination.

Table 3

A three-way analysis of variance testing for differences in total macroalgal biomass and density of thalli in the canopy. Data were square-root (X + 0.5) transformed. Fixed factors: time, depth, and site. n = 6 per sampling event and depth stratum.

Source	d.f.	Total macroalgal biomass g wet-weight 0.25 m⁻²		Density of thalli 0.25 m⁻² for canopy species	
		MS	F	MS	F
Time	3	85.12	2.00	6.27	5.81**
Depth	1	159.72	3.74	93.79	86.93**
Site	1	210.41	4.93*	18.80	17.43**
T x D	3	102.63	2.41	8.67	8.03**
T x S	3	69.47	1.63	4.07	3.78*
D x S	1	613.09	14.37**	29.89	27.71**
T x D x S	3	26.00	0.61	10.88	10.08**
Error	80	42.65		1.08	

*P < 0.05; ** P < 0.01

Table 4

Biomass (mean g wet-weight ± se) of species that contributed > 50 g 0.25 m⁻² in at least one sampling event and depth combination A: southern site, B: south-eastern site. n = 6 per sampling event and depth stratum.

(A) Southern site

Species	Depth (m)	Spring 2002	Autumn 2003	Spring 2003	Autumn 2004
^c*Acrocarpia robusta* (J. Agardh) Womersley	< 10	39 ± 31	73 ± 46	459 ± 377	70 ± 68
	10–20	118 ± 68		45 ± 29	28 ± 27
Caulerpa sedoides C. Agardh f. *geminata* (Harvey) Weber-van Bosse	< 10		43 ± 20	96 ± 38	13 ± 7
Codium mamillosum Harvey	< 10	7 ± 7	*	28 ± 12	*
	10–20	97 ± 35	11 ± 11	72 ± 24	343 ± 63
^c*Cystophora brownii* (Turner) J. Agardh	< 10	297 ± 90	91 ± 67	39 ± 24	164 ± 64
	10–20	66 ± 66			
^c*Cystophora gracilis* Womersley	< 10	160 ± 71	28 ± 13		*
^c*Cystophora monilifera* J. Agardh	10–20	73 ± 36	8 ± 8	14 ± 14	10 ± 7
^c*Cystophora racemosa* (Harvey *ex* Kützing) J. Agardh	10–20		*	222 ± 158	16 ± 16
^c*Cystophora subfarcinata* (Mertens) J. Agardh	< 10	115 ± 43	11 ± 11		82 ± 10
Distromium flabellatum Womersley	< 10	31 ± 10	*	55 ± 12	*
	10–20	24 ± 3	*	*	*
^c*Ecklonia radiata* (C. Agardh) J. Agardh	10–20		73 ± 50	492 ± 268	224 ± 192
Osmundaria prolifera Lamouroux	10–20	200 ± 114			
^c*Sargassum* subgenus *Arthrophycus*	< 10	15 ± 9	39 ± 11		30 ± 21
	10–20	102 ± 56	28 ± 14		30 ± 12
^c*Sargassum decipiens* (R. Brown *ex* Turner) J. Agardh	< 10				413 ± 88
^c*Sargassum spinuligerum* Sonder	< 10			119 ± 35	104 ± 19
	10–20			22 ± 17	*
^c*Scytothalia dorycarpa* (Turner) Greville	< 10		41 ± 41		
	10–20		902 ± 231	57 ± 39	

* < 5 g. ^c = canopy species.

(B) South-eastern site

Species	Depth (m)	Spring 2002	Autumn 2003	Spring 2003	Autumn 2004
^c*Acrocarpia robusta* (J. Agardh) Womersley	< 10	17 ± 11	49 ± 21	158 ± 43	6 ± 3
Amansia pinnatifida Harvey	< 10	64 ± 11			
Botryocladia sonderi Silva	10–20	91 ± 12	91 ± 28	12 ± 8	18 ± 7
^c*Caulocystis uvifera* (C. Agardh) Areschoug	10–20	68 ± 47		7 ± 7	
Cladurus elatus (Sonder) Falkenberg	< 10			264 ± 72	
	10–20	36 ± 24	43 ± 21	*	74 ± 56
Codium mamillosum Harvey	< 10	7 ± 5		116 ± 59	
	10–20	28 ± 24	6 ± 6	32 ± 25	22 ± 12
^c*Cystophora brownii* (Turner) J. Agardh	< 10	681 ± 172	318 ± 126	126 ± 57	28 ± 19
^c*Cystophora gracilis* Womersley	< 10	*	61 ± 33	21 ± 14	*
^c*Cystophora monilifera* J. Agardh	< 10	*	18 ± 14	*	205 ± 64
	10–20		30 ± 30	276 ± 180	234 ± 122
^c*Cystophora subfarcinata* (Mertens) J. Agardh	< 10			12 ± 12	111 ± 96
Laurencia spp.	< 10		61 ± 23	10 ± 5	13 ± 5
Osmundaria prolifera Lamouroux	10–20	49 ± 5	69 ± 12	36 ± 17	52 ± 15
^c*Sargassum spinuligerum* Sonder	< 10	50 ± 23			
	10–20	71 ± 44			
^c*Scaberia agardhii* Greville	< 10	382 ± 90	66 ± 42		530 ± 185
	10–20	40 ± 32	71 ± 67	47 ± 39	63 ± 63
Zonaria spiralis (J. Agardh) Papenfuss	< 10	106 ± 26	*	*	34 ± 14

* < 5 g. ^c = canopy species.

Species that contributed ≥5 g per 0.25 m² included canopy taxa such as species of *Acrocarpia*, *Caulocystis*, *Cystophora*, *Sargassum*, *Ecklonia*, and *Scytothalia* (Table 4).

Density of thalli in the canopy showed no consistent difference between spring and autumn samples (Fig 2), as demonstrated by the significant interactions term "time x depth x site" (Table 3). Density of thalli in the canopy was more variable among sampling times in depths < 10 m than in depths 10 to 20 m (Fig 2). Excluding spring 2002 samples, density of thalli was greatest at the southern site in depths < 10 m (Fig 2).

In depths < 10 m, assemblages showed no unique spring or autumn patterns. Instead, assemblages differed significantly among sampling times (Clarke's R_{time} = 0.89 for southern site, 0.93 for south-eastern site, P = 0.001 for both sites) and between samples collected in the same season (Table 5). Of the 120 species recorded in depths < 10 m, each species was present on average in 7 of the 48 quadrats sampled. Only *Acrocarpia robusta* Womersley and *Cystophora brownii* Turner (J. Agardh) were recorded in every sampling event (season and exposure combination; Table 4).
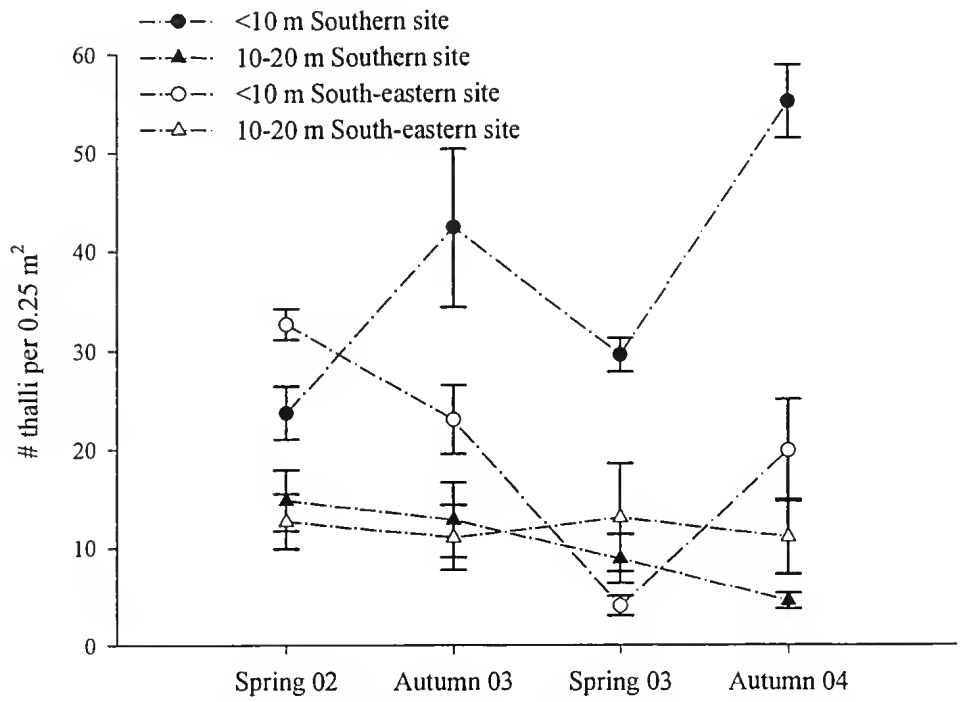
Figure 2. Density of thalli in the canopy per 0.25 m² (mean ± se) per sampling time at Black Island. n = 6 per site and depth stratum combination for each sampling time.

As in depths < 10 m, macroalgal assemblages differed among sampling times in depths 10–20 m (Clarke's R_{time} = 0.72 for southern site, 0.58 for south-eastern site, P = 0.001 for both sites), and between samples collected in the same season (Table 5). Of the 148 species recorded in depths of 10–20 m, each species was present on average in 6 of the 48 quadrats sampled. *Dilophus fastigiatus* (Sonder) J. Agardh and *Laurencia* spp. were present in every sampling event.

A number of species had greater abundances within spring or autumn samples. Because populations were patchy, these patterns remain qualitative. *Cystophora* species generally had greater biomass in spring, particularly in spring 2002 (Table 4). Biomass of *Codium mamillosum* Harvey (except in autumn 2004, southern site) and *Distromium flabellatum* Womersley was also greater in spring samples (Table 4).

Of the species that were fertile at the time of collection, 77% were fertile in both seasons (Table 6). All canopy species were reproductive in autumn and spring (Table 6). Fucalean species in the canopy had partially-depleted conceptacles in autumn.

Table 5

Clarke's R values from pairwise comparisons between sampling times at A: southern site and B: south-eastern site in depths < 10 m and 10–20 m. Comparisons were calculated using analysis of similarity. Biomass data were fourth root transformed. n = 6 per site and depth stratum combination.

(A) Southern site

| | < 10 m | | | 10–20 m | | |
	Spring 2002	Autumn 2003	Spring 2003	Spring 2002	Autumn 2003	Spring 2003
Autumn 2003	0.88*			1.00*		
Spring 2003	1.00*	0.73*		0.75*	0.50**	
Autumn 2004	0.95*	0.82*	1.00*	0.67*	0.91*	0.48***

*P = 0.002, **P = 0.006, ***P = 0.009

(B) South-eastern site

| | < 10 m | | | 10–20 m | | |
	Spring 2002	Autumn 2003	Spring 2003	Spring 2002	Autumn 2003	Spring 2003
Autumn 2003	0.89*			0.96*		
Spring 2003	1.00*	1.00*		0.58*	0.58*	
Autumn 2004	0.90*	0.85*	0.98*	0.64*	0.60*	0.19**

*P = 0.002, ** P = 0.067

Table 6

Fertile specimens collected in autumn and spring from Black Island.

Species	Autumn	Spring
Acrocarpia robusta (J. Agardh) Womersley	*	*
Amphiroa anceps (Lamark) Decaisne	*	
Amphiroa gracilis Harvey	*	*
Caulocystis uvifera (C. Agardh) Areschoug	*	*
Cystophora brownii (Turner) J. Agardh	*	*
Cystophora expansa (Areshoug) Womersley	*	*
Cystophora gracilis Womersley	*	*
Cystophora monilifera J. Agardh	*	*
Cystophora pectinata (Greville and C. Agardh ex. Sonder) J. Agardh	*	
Cystophora racemosa (Harvey *ex* Kützing) J. Agardh	*	*
Cystophora subfarcinata (Mertens) J. Agardh	*	*
Distromium spp.	*	*
Glossophora nigricans (J. Agardh) Womersley		*
Laurencia elata (C. Agardh) J. Hooker and Harvey	*	*
Metagoniolithon radiatum (Lamarck) Ducker	*	*
Metamastophora flabellata (Sonder) Setchell	*	*
Myriodesma harveyanum Nizamuddin and Womersley	*	
Osmundaria prolifera Lamouroux	*	*
Plocamium mertensii (Greville) Harvey	*	*
Polysiphonia decipiens Montagne	*	*
Ptilocladia pulchra Sonder	*	
Sargassum fallax Sonder	*	*
Sargassum heteromorphum J. Agardh	*	*
Sargassum lacerifolium (Turner) C. Agardh	*	*
Sargassum linearifolium (Turner) C. Agardh	*	*
Sargassum spinuligerum Sonder	*	*
Sargassum tristichum Greville and C. Agardh *ex* Sonder	*	*
Scytothalia dorycarpa (Turner) Greville	*	*
Spyridia dasyoides Sonder		*
Wrangelia plumosa Harvey	*	

Discussion

Subtidal macroalgae collected from a temperate southern Australian island showed no clear differences between autumn and spring samples. Instead, differences in assemblages were as great between autumn and spring as interannual differences within each sampled season. The absence of a consistent temporal pattern may be a reflection of little seasonal variability in biological and physical oceanographic parameters. Instead, exposure to wave energy may have a greater influence on species diversity, contributing to the observed species turnover at the metres-scale in autumn and spring. Diversity may be maintained with the removal of macroalgae by year-round exposure to swells > 2 m, and the successful recruitment of macroalgal species whose parent populations release propagules throughout the year or via vegetative recolonization.

Many of the oceanographic parameters measured in the archipelago were appreciably similar throughout the year, which may explain the lack of a distinctive spring or autumn assemblage. Seasonal patterns in subtidal macroalgal diversity have been correlated to periods of high or low seawater temperatures (Nunez-Lopez &Valdez 1998), upwelling periods (Diaz-Pullido and Garzon-Ferreira 2002), and storm activity (Reed & Foster 1984, Breda & Foster 1985). In the Recherche Archipelago, sea-surface temperatures, nutrients (as nominally indicated by chlorophyll a concentrations), salinity, and wave heights were similar throughout the year, albeit in different years than those sampled in this study. Furthermore, the narrow ranges of these environmental factors may contribute to subtidal assemblages in the Recherche Archipelago consisting of perennial canopy (*i.e.*, *Cystophora* spp. and *Sargassum* spp.) and understory (*i.e.*, *Osmundaria prolifera*, *Botryocladia sonderi*, *Codium* spp., *Caulerpa* spp., and *Distromium* spp.) species. The presence of various species throughout the year had also been observed at West Island, South Australia, though algal growth did vary seasonally (Shepherd & Womersley 1970).

Greater variability in the number of canopy individuals in depths < 10 m than in 10–20 m may be a function of wave energy attenuating with depth (Denny & Wethey 2001). Physical disturbance by swells would be greater in depths < 10 m. Removal of macroalgae by wave energy would open up space for recruitment, resulting in a mosaic of individuals that recruited at different times (Dayton *et al.* 1984). Increased opportunity for physical disturbance in conjunction with patchy recruitment may result in the observed greater range of thalli in depths < 10 m than in depths 10–20 m.

Differences between assemblages at the southern and south-eastern sites suggest that exposure to wave energy has a greater influence on diversity than factors associated with temporal variation. Site-specific differences in exposure to wave energy may explain the greater abundance of canopy species *Ecklonia radiata* and *Scytothalia dorycarpa* and indirectly, lower species richness at the southern site in depths 10–20 m. The southern site was more exposed to ocean swell than the south-eastern site which was located within an embayment. The prevalence of *E. radiata* and *S. dorycarpa* at wave-exposed sites has been observed throughout the Recherche Archipelago (Goldberg & Kendrick 2004). Total species richness was lower by as much as 50% where these species were abundant (autumn 2003, 2004, and spring 2003 samples). In contrast, where *E. radiata* and *S. dorycarpa* were not present, species richness was comparable between southern and south-eastern sites in depths 10–20 m (38 species). Lower species richness has been correlated to *E. radiata* abundance elsewhere along the south-western coast of Western Australia (Wernberg *et al.* 2003).

Similar to the findings of Shepherd and Womersley (1970), subtidal macroalgal assemblages at an island located along the southern coast of Australia did not necessarily have a unique spring or autumn assemblage. Because oceanographic parameters did not vary much throughout the year, patterns in macroalgal diversity were most likely driven by factors associated with depth and location along the Black Island. Furthermore, species richness remained high in the face of continual exposure to wave energy, indicating resilience via successful recruitment and growth.

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Tetratheca fordiana (Elaeocarpaceae), a new species from the Pilbara of Western Australia

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Abstract

Tetratheca fordiana R.Butcher is described and compared with similar species. It is the northernmost species of *Tetratheca* in Australia, growing on shale associated with ironstone massive outcrops in the Hamersley Range. Like other ironstone endemics in the genus, this species is highly restricted geographically and is listed as Priority One under the CALM Conservation Codes for Western Australian Flora. A taxonomic key to the Western Australian species of *Tetratheca* with two ovules per locule is provided.

Keywords: *Tetratheca*, Elaeocarpaceae, Pilbara, ironstone endemic.

Introduction

There has been considerable recent research into a number of species of *Tetratheca* endemic on ironstone, following the expansion of mining activities in the Koolyanobbing area of Western Australia. In particular, conservation biology studies and taxonomic revisions have been conducted in *T. aphylla* F.Muell., *T. harperi* F.Muell. and *T. paynterae* Alford, Declared Rare Flora (Atkins 2005) which are restricted to small, disjunct ironstone ranges in this area. From this work, there has emerged the description of new subspecies of *T. aphylla* and *T. paynterae* (Butcher et al., in prep.) as well as new species affiliated to both *T. aphylla* (Butcher et al., in prep.) and *T. harperi* (J. Bull, pers. comm.). In her revision of *Tetratheca*, Thompson (1976) noted that many species have extremely localized distributions and suggested that other species might yet be undiscovered as a consequence of being restricted to isolated, under-collected areas. This prediction has been realised over the past decade with the discovery and description of various taxa from isolated hills in the Eastern Goldfields, as well as *T. chapmanii* Alford, a species endemic on sandstone in the Carnarvon Range, Little Sandy Desert (Alford 1995). *Tetratheca chapmanii* was considered the northernmost species of *Tetratheca* in Western Australia until the discovery of the new species described in this paper. The single and opportunistic collection of *T. fordiana*, which constitutes a range extension for the genus of c. 200 km, further supports Thompson's (1976) theory and it can only be supposed that many new taxa still remain to be discovered in this genus.

A number of highly restricted, endemic species of ironstone or sandstone massive outcrops are known from the Eremaean Botanical Province, and the Pilbara bioregion in particular (Western Australian Herbarium 1998). *Dampiera metallorum*, *D. anonyma*, *Tetratheca* *chapmanii* and *Scaevola* sp. Hamersley Range Basalts are examples of such species, many discovered and described after recent botanical exploration in the region (Alford 1995; Western Australian Herbarium 1998; Lepschi et al. 2004). These species, which often require some level of conservation listing, highlight the need for such mountain ranges to be represented in the conservation estate of Western Australia. *Tetratheca fordiana* is another example of one of these endemics and its description brings the number of named *Tetratheca* species in Western Australia to 27 (Western Australian Herbarium 1998).

Methods

All *Tetratheca* specimens at PERTH were examined for comparison with *T. fordiana*. Due to the dearth of material for this new species, observations and measurements have been made from only the holotype. Stem width and vesture as well as colour notes have been recorded from the herbarium specimen, with foliage and floral measurements taken from reconstituted fragments.

The following taxonomic key is focused on the Western Australian species of *Tetratheca* which typically have the two ovules per locule character. Taxonomic revisions are ongoing in *Tetratheca* and a full, revised key for the genus has not been constructed. Users are referred to Thompson (1976) and Butcher et al. (in prep.) for additional information on species with one ovule per locule.

Taxonomy

Key to species of *Tetratheca* in Western Australia with two ovules per locule

1 Stems winged; ovules variable from 1–5 per locule, usually 3 or 4, rarely 2 (Yallingup, Balingup to Cape Riche) .. **T. affinis**

1: Stems terete to quadrangular; ovules typically one or two per locule

2 Ovules typically one per locule [uniovulate species not considered further]

2: Ovules typically two per locule

3 Stems with an even distribution of erect, red-brown setae

4 Stems densely covered in broad tubercules bearing erect, stout, somewhat evanescent setae; petiole setose; leaves with flat margins; petals white to pale pink with dark pink spots or pale mauve (Koolyanobbing Range) .... *Tetratheca sp. (J.Bull 1)*.

4: Stems densely hispid and with erect, usually persistent setae arising from small tubercles; petiole hispid, lacking setae; leaves with revolute margins; petals dark pink (Hamersley Range) .... *T. fordiana*

3: Stems smooth to minutely tuberculate, usually glabrous or with scattered glandular hairs or retrorse red-brown setae only at base of branches

5 Anther tube 2.5–3 mm long with a conspicuously 2-lipped orifice (Tammin to Norseman) .... *T. efoliata*

5: Anther tube 0.6–2 mm long, the orifice oblique or with a longer inner lip

6 Base of plant usually covered with strongly retrorse, dark setae; peduncle glabrous, pink-green to pink-red, 7–16 mm long; leaves with revolute margins (Wongan Hills to Katanning) .... *T. retrorsa*

6: Base of plant lacking strongly retrorse, dark setae; peduncle scabrous to hispidulous, often with scattered, small glandular hairs, glossy green-red, 1–11 mm long; leaves without revolute margins

7 Stems minutely tuberculate with scattered glandular hairs; calyx segments broadly elliptic (Carnarvon Range) .... *T. chapmanii*

7: Stems densely covered with rounded to truncate tubercles; calyx segments narrowly triangular to lanceolate (NE of Southern Cross) .... *T. paynterae*

Tetratheca fordiana R.Butcher sp. nov.

Caules graciles, 0.6–0.85 mm lati, teres, hispidi, setosi; setae erectae, rubiginosae, 0.3–1.2 mm longae. Folia sparsa, persistentia, 1.5–5.9 mm longa, marginibus revolutis. Pedunculi 3–6.3 mm longi, rosei, pubescentes. Calycis lobi 2.2–2.6 mm longi, 1.5–1.7 mm lati, rosei, ovati, pubescentes, marginibus crassis. Petala 5(6), 8.8–9.7 mm longa, 5.8–6.1 mm lata, elliptica ad obovata, rosea. Stamina 10(12), 4.5–5.5 mm longa, rubra, tuberculis paucis obtecta; filamentum 0.6–1.1 mm longum; corpus 2.2–2.8 mm longus; tubus 1.5–2 mm longus. Ovarium dense appresse pubescens et pilis glandulis dense ornatum; ovula 4, in quoque loculo 2.

Typus: West Angelas area, Hamersley Range [precise location withheld for conservation purposes], WA, 03 Sep. 1987, *N. Casson X7.1* (holo: PERTH 04119630).

Sub-shrub, 0.3–0.4 m in height, with an overall ruby-pink tinge. *Stems* numerous, alternately branched, slender, apices indeterminate but senescing to form a short, blunt, blackened tip, terete, straight, glaucous, terminal branchlets 28–92 mm long, 0.6–0.85 mm wide in flowering region, pinkish-grey hue to younger stems, older stems grey, rugose to broadly striate, densely hispid with an even, moderately dense, covering of short, red-brown, erect setae, 0.3–1.2 mm long, these arising from small, prominent, elliptic, white tubercles that persist on older stems after setae fall. *Leaves* alternate, sparse, +/- adpressed to stem, usually with 2 setae at base +/- in the stipular position, persistent to tardily deciduous; petiole thickened, red, 0.15–0.45 mm long; blade 1.5–5.9 mm long, 0.5–1.3 mm wide, narrowly ovate to linear, predominantly oblong, acute or obtuse, margins thickened to revolute, often appearing dentate due to scattered marginal glandular hairs, apex terminating in a glandular hair or remnant hair base, appearing mucronate; adaxial surface with spreading to ascending, moderately dense simple hairs; abaxial surface paler with shorter, erect, simple hairs, these predominantly on the thickened, reddish mid-vein. *Flowers* single in leaf axils. *Bracts* paired, 1.2–1.4 mm long, 0.5–0.6 mm wide, ovate, hispid adaxially and abaxially, green with pink apex, midvein and petiole. *Peduncles* strongly curved at base, pink-red, 3–6.3 mm long, 0.3–0.6 mm wide, lightly hispid, very finely striate, expanding gradually along length and fluted at apex before expanding suddenly into a receptacle 0.7–1.2 mm wide, receptacle thickened between each calyx segment, appearing lobed when viewed from below. *Calyx* segments 5(6), inserted just inside top of receptacle, with a small horizontal fold just above base and resting on receptacle margin, ovate, acute to obtuse, slightly concave, 2.2–2.6 mm long, 1.5–1.7 mm wide, caducous, sometimes tardily so, pink, with yellow spot at base internally, lightly spreading hispid externally with fine white spots, hairs shorter and more tangled internally, concentrated along margins and visible from outside, as well as at apex and along thickened midvein, with thickened, reflexed margins. *Petals* 5(6), elliptic to obovate, obtuse, 8.8–9.7 mm long, 5.8–6.1 mm wide with the widest point near the middle to 2/3 length, deciduous, dark pink, paler to yellowish at base internally with a darker pink band through the midline. *Stamens* 10(12), 4.5–5.5 mm long, fused into pairs for 1/2–2/3 of the filament; filaments flattened, angled to curved inwards, yellow, 0.6–1.1 mm long; body +/- straight on inner edge, gently curved on outer edge, then contracting, usually abruptly, into the tube; anther cells prominently separated, the upper two broader than the lower two, outer margins of upper cells shortly acute tuberculate, often with scattered, short, simple hairs, margins of lower two cells with short, spreading, simple hairs, dark red, often paler red on lower two cells, 2.2–2.8 mm long; tube usually arising abruptly from junction with body on outer edge, straight to gently sinuous with a narrow, two-lipped orifice, the outer lip longer than the inner, smooth or with a few tubercles at base on inner surface, red at base, fading to yellow at apex, 1.5–2 mm long. *Ovary* flattened, 1.4–1.8 mm long, 1.1–1.2 mm wide, densely covered with ascending, simple hairs and dense, pale coloured or red-tipped, glandular hairs, green but orange-pink towards margins and at base of style, slightly thickened at base; *style* kinked in mid region with short, simple hairs to *c.* 3/4 length, red at base fading to yellow at apex, 2.2–2.9 m long; *ovules* 4, 2 in each locule, the upper ovule attached *c.* 2/3 of the way along axis, the lower ovule attached near middle. *Fruit* compressed-obovoid, 5.8–6.3 mm long, 4.8–5.3 mm wide, red-brown at base, orange-pink at apex, glossy, lightly hispid with scattered glandular hairs or remnant bases. *Seed* cylindrical, 2.75 mm long, 1 mm wide, tapering at base, truncate at apex, +/- flat on axial side, brown; testa very finely striate, pubescent with erect to very slightly
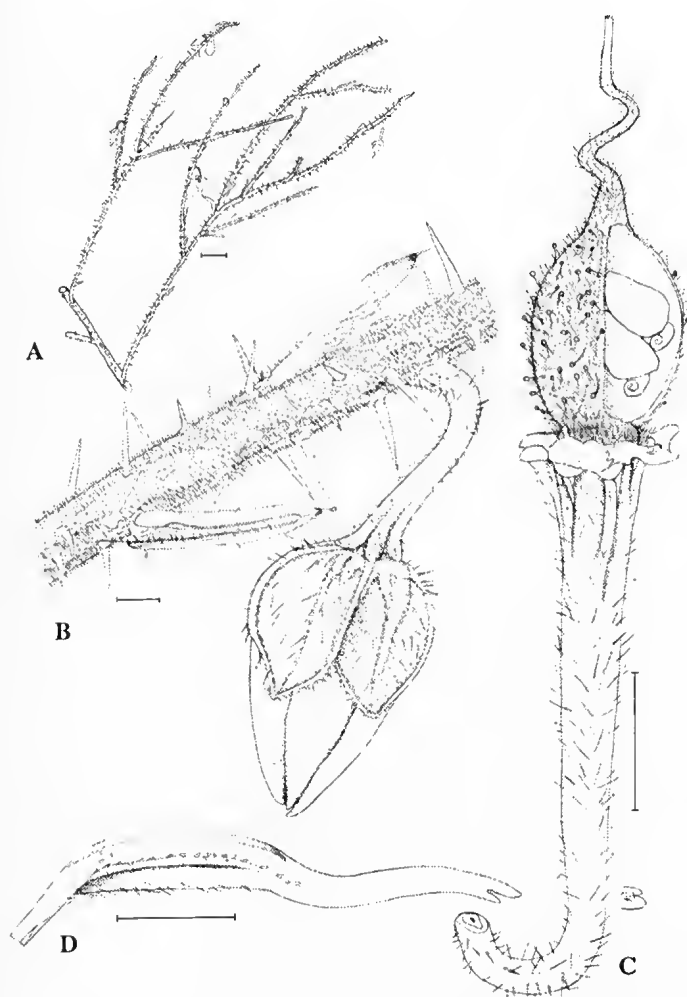
Figure 1 A–D. Illustration of *Tetratheca fordiana*: A – portion of herbarium specimen showing branching pattern; B – portion of stem showing hispid vestiture and tubercle-based setae, leaf arrangement, pubescence and form, and solitary flower bud with ovate, concave calyx segments; C – dissected gynoecium showing dense simple and glandular pubescence on the ovary, two ovules per locule, attached near the middle of the axis, the kinked, pubescent style, as well as the lightly hispid and very finely striate peduncle expanding into a ridged receptacle; D – stamen showing the relative lengths and curvature of the filament, body and tube and the scattered tubercles and simple hairs on the body. Scale bars = 1 cm (A); 1 mm (B–D). Illustrations taken from the holotype.

antrorse simple hairs; *elaiosome* prominent, cream, apparently with broad tubercules along length, +/- terete at base becoming flattened towards apex, irregularly coiled beyond the seed in 2–3 coils, 0.9 mm long in coiled state, with numerous, fine, short, erect hairs. (Figure 1)

Phenology

The holotype was collected in flower and fruit at the start of September.

Specimens examined

Only the holotype has been examined.

Distribution

Tetratheca fordiana is known from only one collection,

from a location in the West Angelas area of the Hamersley Range, in the Pilbara bioregion (Figure 2). Attempts to relocate the species have been unsuccessful.

Regional surveys in the Pilbara, including a specific mountain-top survey, by botanists such as Stephen van Leeuwen and Malcom Trudgen, have not located other populations of the new species. Considering this, and the highly restricted distributions of many other *Tetratheca* species (*e.g.*, *T. chapmanii* of the Carnarvon Range), it is likely that *T. fordiana* occurs only on or near the mountain of the holotype location.

Habitat

Shallow, loose, yellow shale among ironstone on a north-facing buttress, in *Triodia wiseana* hummock grassland with *Eucalyptus kingsmillii*.

Etymology

The specific epithet honours ecologist Douglas Ford, friend and colleague of RB, in thanks for his encouragement and support.

Conservation status

Priority One under the CALM Conservation Codes for the Western Australian Flora (Atkins 2005) is an appropriate ranking for *Tetratheca fordiana*. The new species has been collected only once, from a population of three or four plants (N. Casson pers. comm.), despite a number of specific and regional surveys (S. van Leeuwen & M. Trudgen pers. comm.).

Affinities

Tetratheca fordiana is easily distinguished from all other species by its slender, setose and hispid stems, densely pubescent and glandular hairy ovary, two ovules per locule and its geographic location.
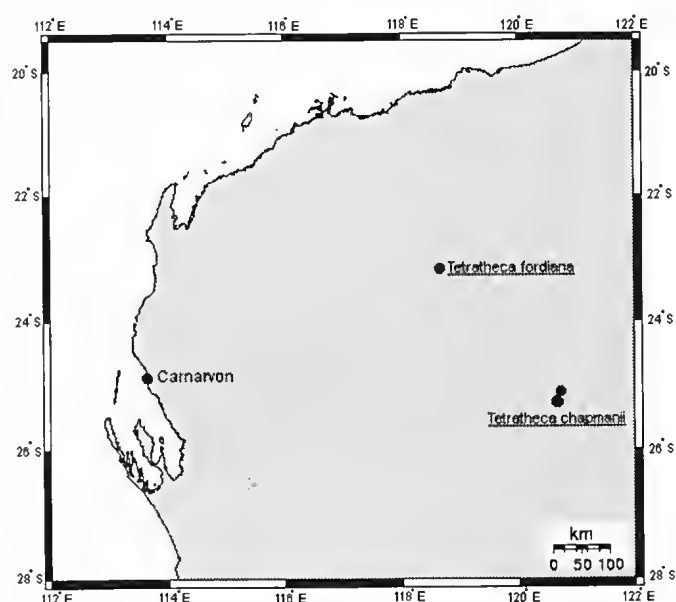
Figure 2. Distribution map for *Tetratheca fordiana*. The single known location of this species is shown relative to the collections of the geographically closest taxon, *T. chapmanii*.

In having two ovules per locule, ovate calyx segments and sparse foliage, *Tetratheca fordiana* resembles *T. chapmanii*, the closest taxon geographically which occurs in the Carnarvon Range, 270 km north of Meekatharra (Alford 1995). Typical specimens of *T. chapmanii* differ from *T. fordiana* in having the stems more or less glabrous except for scattered glandular hairs that are concentrated at the base of the branches, with the same indumentum on its peduncles and calyx segments. Three atypical collections of *T. chapmanii* at PERTH (*K. Coate 455*; *F. Kininworth 24*; *B. & B. Backhouse et al. BEMJ 199*) have hispid stems with a sparse, even distribution of antrorse glandular hairs, but field work and further collections through the Carnarvon Range are required to determine whether these represent a different taxon. Unlike *T. fordiana*, the leaves of *T. chapmanii* are caducous, small (*c.* 1.7 mm long) and triangular, with flat margins, and the affinities of this species appear to lie closer to *T. paynterae*, another 'leafless' species with two ovules per locule that occurs north-east of Southern Cross in the Coolgardie Botanical District (Alford 1995). Although the 'leafless' condition is evidently the result of convergent evolution (Butcher *et al.* in prep.) a comprehensive phylogenetic analysis must be made to assess the affinities between all the species of *Tetratheca* and to ascertain the significance of ovule number as an indicator of relationships.

Tetratheca harperi and *Tetratheca* sp. (*J. Bull 1*) are similar to *T. fordiana* in having glaucous stems covered with erect, coarse setae, but the stems are thicker in these two species, the setae are denser and arise from much broader tubercles, and hispid simple hairs are absent. Of these two species, a closer relationship might be hypothesised between *Tetratheca* sp. (*J. Bull 1*) and *T. fordiana* based on ovule number, with each of these species having two ovules per locule while *T. harperi* has only one. Stamen morphology and vesiture is also similar between these three taxa, but they differ significantly in the pubescence of the gynoecium; *T. harperi* and *Tetratheca* sp. (*J. Bull 1*) having a glabrous ovary and a +/- straight, glabrous style, while *T. fordiana* has the ovary densely covered in both simple and glandular hairs, and has a distinctly kinked style with short, simple hairs to *c.* 3/4 of its length.

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Honorary Editor's Preface

In March 2004, a Workshop on "Preventing wetland soils and sediments from burning on the Swan Coastal Plain" was convened by Dr Pierre Horwitz from Edith Cowan University (ECU) and Ralph Smith from the Fire and Emergency Services Authority (FESA). Later in 2004, the convenors approached the Royal Society of Western Australia with the view to publishing the Workshop Proceedings through the Society's Journal as a Thematic Issue. The Royal Society of Western Australia agreed to producing a Special Issue for this work which would further the advancement of Science, promote a general community and scientific awareness of the important matters raised in relation to fires in wetlands, and assist in the dissemination of the information presented at the Workshop. All the papers have undergone the normal peer review process, but have been tailored to appeal to a general scientific community rather than a specialised audience, and are a stand alone collection of papers covering the key issues associated with fire in wetlands on the Swan Coastal Plain. In essence, this Special Issue presents a variety of papers that touch on the main issues associated with the burning of peat and soils in wetlands, from a range of perspectives: from the general setting and importance of peatlands, to the natural features of peaty wetlands, to community health, to fire management. The Royal Society of Western Australia hopes that the information herein will lead to a heightened awareness and appreciation of the issues that relate to better management of fires in the specialised ecosystems that comprise peaty wetlands on the Swan Coastal Plain.

The cover has been designed to capture the spirit of this Special Issue. The upper illustration, a ternary diagram from Semeniuk & Semeniuk, shows an empirically derived boundary between flammable and non-flammable wetland substrates. The middle photograph from the Jones paper shows a burnt-out stolen vehicle, abandoned and set alight by arsonists, which formed a blaze that was the source of the fire in the wetland adjoining the track. The lower photograph, from Horwitz & Sommer, shows a very localised circular burnt patch of wetland soil centred on a *Melaleuca* shrub in Lake Mariginiup, with post-fire recovery of sedges.

Kathy Meney
Honorary Editor
Royal Society of Western Australia

Fire and wetland soils and sediments on the Swan Coastal Plain: an Introduction

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Abstract

This Special Issue of the Journal deals with the interactions between fires and wetlands, focusing on particular wetland soils and sediments of the Swan Coastal Plain bioregion that have a propensity to burn. In doing so, contributing authors cover the type of information required to understand those influences, like the nature of the soils and sediments themselves, the implications of the fires for environmental, social and economic values, and how the fires might be prevented.

Keywords: fire, organic soils, climate change, groundwater decline, fire suppression

Introduction

The topic of fire and wetland soils and sediments might seem odd at face value. Organic-rich soils, often called 'peats', are formed mostly under permanently saturated conditions and these are precisely the conditions that should make their combustion difficult. While wet organic soil can combust, and burn for long periods of time at high temperatures, they only do so only under rare conditions of ignition. However, if the soils dry out, they become much more susceptible, and the hundreds if not thousands of years of accumulated organic material stored in the wetland sediments can become regularly exposed to the direct effects of a fire. The topic therefore raises issues that are both specific and general. The fact that wetland soils and sediments (in particular those that are organic-rich) are becoming more vulnerable to fire on the Swan Coastal Plain, highlights the changing nature of its environment as land use changes from bushland, silviculture and horticulture, to peri-urban development, accommodating urban expansion.

These circumstances of vulnerability currently operate on the Swan Coastal Plain, and invoke the following important considerations:

- the climatic conditions that lead to a drying of wetland soils instead of them being subject to winter inundation and summer saturation;

- added reasons for the groundwater decline such as groundwater abstraction for silviculture, horticulture and domestic urban use; and

- the proximity of susceptible wetland soils and sediments to areas of human habitation, and human sources of ignition.

The impacts of fires in organic-rich soils cover issues of biodiversity, air quality, water quality and risk to humans including fire and emergency personnel, and risk to property.

The topic extends from fire management to human health, water quality, land use, urban development and climate change, and the case study of the Swan Coastal Plain is therefore useful to similar scenarios being encountered in other parts of Australia and the world.

Fire suppression and research needs

Bush fires that occur in the dry organic-rich soils have the potential to burn for extensive periods, burning through the soil on the surface or as a subterranean fire. If subterranean, the fire will generally require the break of the season, and for substantial winter rains, to raise the soil moisture content to a level that will suppress the burning fire. As these fires are frequently subterranean, fire fighters can have difficulty in identifying the area that requires suppression, until the fire comes to the surface.

These types of fires are occurring in discontinuous remnant areas, and environmentally sensitive zones, within the Swan Coastal Plain, the most densely populated area within Western Australia. Flora and fauna contained within these remnant areas are potentially at threat of local extinction if they are subject to burning and subsequent soil loss, water quality changes or hydrological change.

Bush fire suppression in wetlands provides the fire responders with significant conundrums. These are, the fire itself, if left to burn it can cause social problems through the smoke that is generated for extended periods, and the potential safety problems, where the subterranean fires are not always visible to the naked eye. If fire suppressants are used they may adversely affect biodiversity in the wetlands and adjacent areas. If a machine is used to create a physical break there are potential implications for acidification of the soil and also the obvious physical impact that occurs.

Preventing the soils from burning therefore is the preferred method of protecting the organic soils. This is a very complex option as it is dependent on preventing bush fire arson, accidental fires or escapes from burning in adjacent areas. Managing and controlling human behaviour by its very nature is complex.

For all these reasons a research focus on fires in wetland soils and sediments, and their management, is timely.

Past research

While some scientific information on the biology, composition and location of wetlands with organic-rich soils and sediments on the Swan Coastal Plain is available, there are a number of gaps. Indeed the history of this scientific information is interesting. Early research centred around the description of soils for agriculture, and Teakle & Southern's (1937) treatise on the occurrence and properties of peats and other poorly drained soils understandably focused on coastal areas of southwestern Australia, estimating then that upwards of 5% of the coastal sandhill zone could be classified as these types. These authors appeared to be well aware of peat fires:

> The burning of peat lands is practiced universally where agricultural development is being attempted, and a light surface burning is found to be beneficial to the succeeding crops. Deep burning is very deleterious and any burning causes the waste of valuable peat, lowers the surface, restricts the way of life of the formation, and enhances engineering problems. (p. 336).

Later, Simpson (1939) documents the effects of a fire in diatomaceous earth at Spectacles Swamp, south of Perth, including comments on the stratigraphy and the geochemistry of the soils. Intriguingly, both Teakle & Southern (1937) and Simpson (1939), mentioned the potential problems with acid waters associated with these types of soils.

During and after the Second World War wetlands seemed to have received substantially less attention until the late 1970s. Even then, and throughout a period in which increasing attention was focused on wetlands of the Swan Coastal Plain (see for instance, Semeniuk 1987, Balla 1994, Hill et al. 1996, Davis & Froend 1999), little or no effort was devoted to the description of organic-rich soils or sediments per se, or highlighting their vulnerability to fire. While the effects of fires may have been obvious to those with a trained eye (see Semeniuk & Semeniuk, 2005, this issue), the issues remained obscured until the connection between drying of wetland soils and sediments and both acidity (Sommer & Horwitz 2001) and vulnerability to fire (Horwitz & Benier 2003) were raised explicitly following severe drought in the mid-late 1990s.

Subject matter covered in this Special Issue

The Fire and Emergency Services Authority of Western Australia (FESA) and Edith Cowan University (ECU) identified a need for closer attention to the issues noted above from their perspectives of fire prevention and response, and wetland research and management expertise, respectively, sharing a common concern over the potential adverse effects bush fires may have on the very important scattered remnant organic-rich soils and also the built and natural environment communities on the Swan Coastal Plain. The partnership was both relevant and fruitful: joining together to facilitate a workshop in March 2004 that had specialist guest speakers and an audience of participants from key fire, land management, local government and community representatives. These proceedings are the result.

In order to place the organic-rich soils and sediments of the Swan Coastal Plain in an international context, Pemberton (2005, this issue) gives an overview of distribution and formation of peatlands in Australia, as well as their biodiversity and geodiversity values, and general classification of such soils. In a landmark paper on the subject, Semeniuk & Semeniuk (2005, this issue) describe aspects of the organic carbon content, mineralogy, geochemistry and biochemistry of wetland soils and sediments. They argue that along with their hydrology, the potential of the soils and sediments to combust is relative to annual water table fluctuations and longer term climatic patterns, the distribution of flammable material across a wetland, and the nature of stratigraphic interlayering along wetland margins. These issues are then overlain at broader scales by the distribution of wetland sediment types both across the Swan Coastal Plain and along the climatic gradient of the length of the Swan Coastal Plain.

The next three papers focus on the effects of fire in these soils and sediments. Horwitz & Sommer (2005, this issue) review national and international literature to demonstrate the potential for fire to alter the physical and chemical attributes of surface water and groundwater. They describe pathways of influence including catchment effects from runoff and deposition, atmospheric effects (the return to ground of volatilized reactive and particulate compounds), and the rehydration of burnt or overheated soils. Superimposed on these effects are the water quality responses to the trophic consequences of a fire. In addition, fire suppression activities like water bombing, fire retardants and ditching and flooding, all have water quality consequences. In a paper on biodiversity values of organic rich wetland soils or sediments, and focusing mostly on the better known biotic groups like the invertebrates, Pinder (2005, this issue) argues that most species inhabiting wetlands with peaty sediments of the Swan Coastal Plain will be widespread and occur in other types of wetlands on the plain and usually elsewhere. However, he suggested that for a range of species that are otherwise rare or otherwise absent on the SCP, such wetlands provide moist refuges in a generally xeric region. Particularly important habitats include the springs which have mounded accumulations of organic matter.

In their review of air quality following a fire in a peatland, Hinwood & Rodriguez (2005, this issue) describe the constituent characteristics of peat smoke (gases include carbon monoxide, carbon dioxide, nitrogen oxides, sulphur oxides, carbonyl compounds, polycyclic aromatic hydrocarbons and other irritant and hazardous volatile organic compounds). The authors present a review of information available on adverse health effects, notably respiratory diseases and

symptoms, and highlight a need for more appropriate epidemiological data to be gathered.

Added to these issues are the practical ones of dealing with a fire in a peatland. In a paper from a fire manager's perspective, Jones (2005, this issue) describes the specific dangers and logistic difficulties associated with managing such fires, highlighting matters such as access to the wetland and the fire, inappropriate equipment, and the possibility of injuries for firefighters.

The papers presented at the workshop allowed participants opportunity for around-the-table discussions to address key questions concerning fire protection and fire prevention for these organic rich soils and sediments, and these recommendations are found in the workshop summary paper, the final paper in this issue.

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Australian peatlands: a brief consideration of their origin, distribution, natural values and threats

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Abstract

Peatlands cover a very restricted area of the earth's surface. Their total reliance on water to maintain natural processes make them highly significant terrestrial ecosystems. They are typically biologically hostile environments due to waterlogging, low pH and anaerobic conditions. The most extensive peatlands occur in the maritime and Tundra areas of the Northern Hemisphere, although tropical peats contain large volumes of peat. Peatlands in Australia are restricted and are rare due to the prevailing environmental conditions in this country. Nevertheless there are highly significant and unique peatlands with few similarities to those in other parts of the world. The natural diversity (geodiversity and biodiversity) of Australian peatlands needs to be investigated and recognised in order to understand, manage and protect these vulnerable environments. They are under increasing pressure from human development and climate change. A better understanding of their distribution, conservation status and hydrological characteristics would contribute to their protection and conservation.

Keywords: Australian peatlands, distribution, origin, threats, classification, geodiversity.

Introduction

Peatlands cover about 5 % of the earth's surface (Gorham 1991). Humans have used peatlands and peat for thousands of years. They have lived in houses cut from peat, used it as a fuel, used it in powerplants, made beer and whisky with it, and used it for medicinal purposes or as sacrificial depositories.

Peat cutters in northern European bogs have discovered numerous human fossils in peatlands. Pete Marsh or Lindow Man, the bog body discovered in the United Kingdom in the 1980's was bludgeoned with an axe, garrotted, stabbed with a long thin blade that was plunged into his throat and finally thrown into a bog (Stead *et al* 1986). It was his presence in such fine condition, including intact nails, hair and skin which was testimony to the anaerobic conditions typical of peat areas, slow rates of decomposition, the lack of animal decomposers and the generous nature of his Celtic brethren who offered him as a sacrifice. Celtic people often threw offerings to the gods into rivers and mires and it is even thought that Pete may have been a druid who could consider it a great honour to have died in such a fashion (Stead *et al* 1986). The oldest bog body, Koelbjerg woman died 8000 years ago at the age of about 25 (Stead *et al* 1986). She did not have an axe hole in her head or a garrotte intact, but appears to have died from drowning.

Peatlands can be threatening to many living things. They are wet, soggy, hostile environments which *Homo sapiens* and many plants and animals find inhospitable unless they are specially adapted to cope with the conditions (Maltby *et al* 1992).

Peatlands could be described as being analogous to living organisms because they grow, mature and can die quite naturally. This could be a response to a loss of water supply or change in preferred climatic conditions (Moore & Bellamy 1974). It is also quite likely that peat deposits do not just grow and develop at an even rate. There can be changes which result in a decrease or increase in plant growth and organic accumulation, or a change in the type of plants which develop at particular sites.

Peatlands are unusual terrestrial ecosystems being composed of up to 90 % water. The environmental conditions in peatlands are often harsh with very low pH, low dissolved oxygen levels and very low nutrient levels (Lindsay 1995). In some instances nutrients may be imported into the peatlands by groundwater. They are different to other terrestrial ecosystems primarily because organic matter accumulates at a greater rate than it can decompose.

Peatlands pose research and management challenges to land managers, fire managers, planners and natural scientists (geomorphologists, ecologists, pedologists, hydrologists, botanists, and zoologists). This is because the processes which operate in these ecosystems are quite different to most other terrestrial ecosystems.

Water is important to all ecosystems, or at least to life in all ecosystems. In peatlands it is critical to the natural processes which control the way they function (Hughes & Heathwaite 1995). They must be wet for long periods and would rapidly decline if deprived of water.

Peatlands are intricately linked to water (Bragg 2002) whether it is groundwater in areas that receive very little rain or rain where there is little to no groundwater. Peatland hydrology is often poorly understood, even in

areas with far more extensive peatlands than Australia (Moore & Bellamy 1974). In this country this is an important consideration, given climate change and particularly the demand for water, which can impact directly on these, typically marginal ecosystems.

They can be considered as geological/ geomorphological deposits, wetlands, water bodies, wasteland or just land. There is often a confusion of terminology relating to the different disciplines, which investigate these ecosystems. Their uses can be wide ranging from agriculture, forestry, fuel production, pollution control, recreation, tourism, nature conservation and scientific research.

The objectives of this paper are to provide an overview of peatland terminology where they occur in Australia, how they have developed and the wide range of threats posed to their natural values.

Terminology, classification and definitions

There are clearly acknowledged difficulties in peatland classification given the broad range of disciplines interested in these ecosystems. Charman (2002) has argued that the classification of peatlands is one of the most fraught and misunderstood taxonomic systems of all. Moore (1984) has indicated that this is probably because there are so many criteria which can be used, and almost all of them are continuous rather than discrete variables. Many countries with peatlands have developed classification systems of their own and few are identical or similar in detail. There are however common elements such as the predominance of water logging, high organic contents and chemical conditions, which can be hostile to flora and fauna.

According to Gore (1983) the general term to cover ecosystems referred to as swamp, bog, fen, moor, muskeg and peatland is mire. There appears to be some interchange between peatland and mire in Gore (1983) and for the purposes of this discussion the term peatland will be used to describe these ecosystems. The distinguishing feature they typically have is that they are usually underlain by, or consist of peat.

Gore (1983) further recommends subdivision of mire into fen and bog. Bog generally refers to mineral poor peatlands with low pH, while fens are less acid or possibly alkaline and mineral rich peatlands. There is no reference to pH limits although Wheeler & Proctor (2000) suggest bogs have a pH of < 5.0 and fens have a pH > 6.0. No explanation is made of peatlands with a pH between 5.0 and 6.0.

The bog/fen division is to a considerable extent based on the origin of the water and its chemistry. Bogs are rain fed and ombrotrophic, the nutrients being supplied predominantly from rainwater, while fens are more likely to be fed by groundwater derived from bedrock or soils, but also by lakes or rivers (Gore 1983). Nitrogen and phosphorous are generally the limiting nutrients with both elements lower in bogs than in fens although no limits have been defined (Wheeler & Proctor 2000).

Peatlands can be classified according to their shape or morphology (*e.g.,* raised bogs and blanket bogs), chemistry (origin and chemistry of water supply), botanical composition (broad distinctions include moss, herbaceous and woody), hydrology (source and flow of water), peat characteristics (for example the degree of humification) and, related to this, stratigraphy (Charman 2002). Classification may depend on what the classification is to be used for but the hydrological approach may be the most appropriate given the significance of water in peatlands. Combinations such as hydrotopographic classifications have also been developed (Gore 1983).

Little attempt has been made to classify peatlands in Australia, which is not surprising, given their limited extent and the lack of systematic scientific work. Most classifications have been developed for the Northern Hemisphere and have little relevance to Australia. This is probably a consequence of the different environmental and climatic conditions between the two hemispheres.

From a soil perspective peats are typically referred to as organic soils or organosols. Organosol (Isbell 2002) is now the preferred term for Australian peats. This class of soils caters for most soils dominated by organic materials. Data on these soils are limited in Australia and that there have been few previous attempts to subdivide them (Isbell 2002).

Organosols are "Soils that are not regularly inundated by saline tidal waters and either:

1. have more than 0.4 m of organic materials within the upper 0.8 m. The required thickness may either extend down from the surface or be taken cumulatively within the upper 0.8 m; or

2. have organic materials extending from the surface to a minimum depth of 0.1 m; these either directly overlie rock or other hard layers, partially weathered or decomposed rock or saprolite, or overlie fragmental material such as gravel, cobbles or stones in which the interstices are filled or partially filled with organic material. In some soils there may be layers of humose and/or melacic horizon material underlying the organic materials and overlying the substrate." (Isbell 2002).

See Appendix 1 for definitions of organic materials and see Isbell (2002) for other definitions relevant to organic rich soil horizons which are not generally referred to as peat.

Organosol profiles can be further divided into the suborders fibric (generally at the top of the profile), hemic (generally in the middle of the profile) and sapric (generally at the base of the profile) which are terms applying to the level of decomposition with less decomposed material at the top of the profile and more decomposed towards the bottom. All suborders do not necessarily occur in a particular soil profile. See Appendix 1 for definition of suborders.

This terminology is similar to the terminology used in Canada, England and Wales (Isbell 2002). Organosols are then further divided into great groups and subgroups, which are presented in Isbell (2002).

Different disciplines treat peat classification in a variety of ways. For example, in other areas of the earth sciences, sedimentary geologists would simply call peats a sedimentary deposit which may then grade, through diagenesis or low grade metamorphism, to organic sediments and finally coal seams.

A brief consideration of world peatlands

Peatlands have characteristically received little attention from the international conservation community, but due to a drastic reduction in their extent in the Northern Hemisphere, this is starting to change. The impact of the 1997/98 peat fires in Indonesia also drew attention to how critical peatlands are for carbon storage and sequestration.

At the international level, peatlands have principally been recognised for their wetland conservation values due to their importance as habitats for waterbirds and particular flora species. This was the driving force for the Ramsar Convention. Peatlands are the most widespread of all wetland types in the world comprising 50 to 70 % of global wetlands (Pastor et al 2003).

The total area of peatland in the world is not known with any accuracy (Charman 2002) but is estimated to be about 5 % (Gorham 1991). This includes approximately 15 % of boreal and subarctic regions (Bridgham et al 2001). As a consequence of climatic and topographic controls the large majority occur in the northern temperate zone and around the equator. Canada, Russia, Sweden and Finland dominate the temperate world peatland areas, while Indonesia, Malaysia and Brazil have the greatest extent of peatland in the equatorial zone. Pfadenhauer et al (1993), Immirzi et al (1992) and Lappalainen (1996) provide good accounts of the extent and composition of the world's peatlands. Difficulties in worldwide estimates are a consequence of the differences in definitions and terminologies applied in different countries. Immirzi et al (1992) estimate the total world extent at around 400 million ha. This is most likely an underestimation given the lack of data from Africa, tropical peats and even Australia, which has relatively small areas of peatland. For example, the blanket bogs of western Tasmania are very rarely referred to in the international literature despite the fact that they cover about 1 000 000 ha (see below) and are by far the most extensive peatlands in the country and possibly the southern hemisphere.

Peatlands in the Northern Hemisphere have been widely impacted by land use change and exploitation including commercial exploitation for fuel, forestry, overgrazing, burning, moorland drainage and acid precipitation (Lindsay 1995). It is estimated that only 10 % of the original area of blanket bogs in Britain remain in a more or less natural state (Lindsay 1995) and there is a major concern that extensive blanket bogs in eastern Europe are threatened by the eastward expansion of mining companies with all the bogs in the Netherlands and Poland lost. Similarly Ireland has 19 % of its original bog area left intact (Lindsay 1995).

Australian peatlands and their palaeoenvironmental constraints

Australian peatlands are found from the wet tropics in the north to the temperate zone, the alpine regions in the south east (Whinam & Hope in prep) to the coastal plains in the south west. Their occurrence is restricted except in Tasmania where the blanket bogs in the west of the State, considered to be the most extensive in the southern hemisphere (Pemberton 1993, Pemberton & Cullen 1995), cover about 1 000 000 ha. In general, however, peatlands are rare in Australia.

Many of the peatlands are peculiar to the continent, or at least the Australasian region, given the processes which have lead to their development, whilst there are some which have Northern Hemisphere counterparts such as *Sphagnum* bogs, sedge fens and *Phragmites-Typha* riparian fens (Whinam et al 1989, Clarke & Martin 1999, Crowley & Gagan 1995). Australian peatlands fall into coastal and montane regions with the mound springs in central areas some of the most peculiar from a peatland perspective (Boyd 1990a, 1990b). Peatlands associated with deflation hollow wetlands are probably fairly widespread although they are not very well documented.

The vast majority of Australian peatlands are late Pleistocene to Holocene in age with most having formed in the last 15 000 years following the last Pleistocene glaciation (Bowler et al 1976). In south eastern Australia this corresponded to the onset of more humid and maritime/temperate conditions following climatic change.

Montane and Tasmanian lowland areas

Highland areas in south eastern Australia provided ideal locations for the development of peatlands following deglaciation. Topographic depressions formed by ice action resulting in the development of cirques, knock and lochan landscapes, nivation hollows and glacial valleys created the on ground conditions suitable for peat accumulation. The cool relatively wet conditions with low evaporation are also conducive to organic accumulation. These are most widespread in the Tasmanian highlands and the Australian Alps (Hope 2003).

Tasmanian blanket bogs occur down to sea level on the west coast of the State, often beyond the range of the most recent ice and glacial action (Pemberton 1993, Pemberton & Cullen 1995). These have formed in response to wet, humid conditions with low evaporation and cover undulating flats to steeper slopes forming a semi-continuos blanket. They are typically only 30 cm deep. In topographic depressions occasional 4 m deep profiles occur (Pemberton 1993). Lowland peatlands also occur on Macquarie Island (Rich 1996) with the greatest depths approaching 6 m.

Sphagnum peatlands are extremely restricted in Australia occurring in isolated parts of Tasmania (Whinam et al 1989), Victoria, New South Wales and the ACT (Clarke & Martin 1999). These are often associated with glaciated terrain in Tasmania where they can be over 4 m deep (Pemberton 1986).

The montane swamps of eastern Australia occur in similar areas and are more widespread but do not occur in previously glaciated country. These are composed of fens dominated by sedges and other restionaceous species which can be highly productive with up to 6 m of peat having formed in 3000 years (Hope 2003). These are arguably some of the most productive peatlands in the country.

Coastal regions

The Post Marine Transgression occurred from 12 000 to 6 000 years ago as sea levels rose following the last glaciation (Thom & Chappell 1975). Sea levels stabilised

around 6000 years ago and have remained relatively stable since this time, a period referred to as the Holocene stillstand (Thom & Roy 1983). The rapidly rising (some suggest a rise of 1.5 m every 100 years) sea levels before the stillstand reworked sandy coastal landforms inland (Thom & Roy 1985). Following the stillstand many coastal dune systems experienced a period of rapid accretion or growth (Thom & Roy 1983). The development of a new series of dune fields also created conditions for the development of dune barred lakes/swamps, which resulted in the formation of peatlands. Former valley systems were flooded creating a variety of conditions around the Australian coast for peat accumulation. Permanent or frequent inundation in estuaries and lagoons provided ideal environments for organic accumulation.

The dune barred and estuarine peatlands in temperate Australia include a variety of forms. Interdune swales contain sedge swamps and lakes. The waterbodies can have peat floors where organic matter has collected helping to form an impermeable substrate.

Excellent examples of perched lakes occur in the Fraser Island dunefields and the Cooloola sandmass in southern Queensland (Longmore & Heijnis 1999). The Fraser Island peats exceed 100 000 years in age while the Cape Flattery dunefields have peats dated at 30 000 years. These typically have shallow peat deposits and are derived from Cyperaceous and Restionaceous vegetation.

The large "permanent" wetlands on the Swan Coastal Plain, Western Australia fall into the coastal peatland category. They are associated with groundwater aquifers where the deep sandy soils are regularly if not permanently saturated (Hill et al 1996). The organic build up is from Cyperaceae and Myrtaceae vegetation whilst the wetland shapes are controlled to some extent by Pleistocene dunes systems (Semeniuk 1988).

In tropical Australia, peat accumulation in coastal sites occurs in similar locations such as interdune swales, but also in mangrove swamps (Crowley & Gagan 1995). True mangrove peat is rare requiring sheltered locations where restricted water circulation prevents flushing.

The broad floodplains on the tropical river systems have organic accumulation in the lagoons inland from the main channel formed under *Melaleuca* forest. They are typically thin deposits with high mineral content (Lees & Saenger 1989).

Rivers along the lower coastal plains of southern Australia also have peat deposits although in the east most of these have been cleared. Some of the best examples are the sedgeland and *Melaleuca* thickets in the south west of Western Australia (Hodkin & Clark 1988). Paper bark communities in northern Tasmania, including the Furneaux Group (Harris et al 2001) and King Island (Barnes et al 2002), have well developed peat profiles. The coastal wallum (sand heath) of north east New South Wales and south east Queensland also fall into the coastal peatland category, which provide relatively long sedimentary records for coastal sea level fluctuations and environmental change (Woodroffe 2003).

In tropical Australia, conditions are generally not conducive to organic accumulation due to seasonal drought and high rates of decomposition. Where conditions are favourable, significant build up can occur, such as in the relatively cool, wet conditions on the Atherton Tableland where some of the best know accumulations of tropical peat occur. These are also the oldest known peats in the country and are probably older than 200 000 years. These form in the low broad volcanic craters referred to as Maars (Whinam & Hope in prep).

Desert peatlands

Perhaps some of the most peculiar peatlands are associated with the spring mounds of the Great Artesian Basin (Boyd 1990a). The fresh water flowing from these permanent point sources in a largely waterless environment generally evaporates or soaks into the soil within tens or hundreds of metres of the springs. There is sometimes sufficient water to form permanent swamps with peat, such as the dramatic examples at Dalhousie Springs (Boyd 1990b) in the Witjira National Park close to the Simpson Desert. This area receives about 100 mm of rainfall per annum. The contrast with the surrounding rock covered plains and saltbush is dramatic.

Deflation hollows

Peatlands developed in deflation hollow wetlands have not been described in great detail in Australia but occur in the midlands of Tasmania, on Cape Barren Island in the Bass Strait (Lazarus & Jerie 2004) and in parts of Western Australia (Horwitz et al 1997). They most likely occur in other deflation hollow complexes around the country such as in the Monaro (Bowler 1983).

Geodiversity and natural diversity

This section specifically addresses the issue of conserving geodiversity in peatlands. Issues considered are the significant relationship, which occur between geodiversity and biodiversity in peatland processes and conservation.

To conserve peatland values all natural values should be considered. There has been a tendency in nature conservation to concentrate on biodiversity when conservation values are being assessed (Eberhard 1997). Geodiversity (see Appendix 2 for definition) is an integral part of peatlands, whether it is in the foundations of the landforms providing the on ground conditions for organic accumulation such as impeded drainage, or in the peatland proper where organic accumulation is occurring. There is a very close relationship between the physical processes influencing peatland development and the contribution that is made by plant material. There is therefore a strong link between abiotic and biotic processes in the formation and maintenance of peatlands.

Direct influences from landforms in peatland development include providing restricted drainage which creates the waterlogged conditions needed for peatlands. This can be provided by glaciated landscapes, dune barred lakes, deflation hollow/lunette complexes or accreting floodplains. These provide the environment for organic accumulation, which in turn provides the foundations for further plant growth and biological activity. Geoconservation values are usually intricately linked with the functioning of the ecosystems and their biological values. Management and conservation of these

ecosystems must consider all these aspects of functioning peatlands.

The conservation arguments for the protection of geodiversity can be very strong. Disturbance or removal of most earth features is normally permanent unless there is a willingness to look at sustainability over thousands or millions of years, and even this does not allow for the re-creation of features that may have formed under particular geological or climatological conditions. In general, peat formation is so slow that any damage to the deposit or long term change to the processes responsible for organic accumulation, are likely to compromise the integrity of the peatland.

Intact peatlands that are accumulating organic matter are valuable palaeoenvironmental archives. They can be used for reconstructing past landscape change, climate change and to document the timing of environmental contamination across the world (Pastor et al 2003).

Conserving peatland values should not concentrate only on areas of maximum diversity and it could be that the extent of a particular peatland type or process is significant from a conservation perspective because of their uniformity. Peatland conservation should include the representative range of peatland types, which in turn requires a comprehensive peatland classification.

Peatland conservation and management needs to comprise more of the peatland than its physical boundaries given the complexities of the hydrological relationships in these environments. This should include the entire peatland catchment.

Threats and conservation considerations

Peatlands have characteristics such as high organic contents that make them vulnerable to fire, climatic constraints such as moisture availability that put them at risk from climate change, a reliance on high water tables that result in threats from ground water extraction and high water retention characteristics which results in a demand for the organic matter from the horticultural industry.

Fire

Fire is one of the major threats to Australian peatlands. In contrast to many other parts of the Australian environment fire can completely destroy peatland ecosystems. Recovery may be considerably retarded following a severe peat fire. Despite this, research into the relationship between fire, vegetation dynamics and organic accumulation in Australian peatlands has been limited.

This contrasts with the Northern Hemisphere, which has more extensive peatlands, but less of a fire adapted landscape with lower fire frequencies. Despite this, fire has impacted on extensive areas of peatland (Radley 1965), including areas of permanently frozen ground. Bower (1959) and Tallis (1973, 1985 and 1987) have studied, in considerable detail, the impact of fire on peatlands of the southern Pennines. Racine (1979) did a comprehensive investigation of 360 000 ha of maritime tundra in Alaska affected by fire. It was estimated that about half of the organic soil had been removed by fire and revegetation was very slow. This affected permafrosted soils and increased thaw depths in summer. In some places blistering occurred on the soil surface as a result of steam produced from melting permafrost. It appears likely that this type of peat burn would have considerable impact on the physical and chemical nature of the soil.

Maltby et al (1990) report that, in the north York moors, fire burnt deeply into blanket peat, and largely destroyed thinner peat reducing it, in the most extreme cases, to a layer of ash. Lindsay et al (1995) considers that burning is recognised as a major initiator of erosion in the Peak District of northern England where problems of peat erosion are extreme in places.

Peatlands are potentially unstable terrains because the organic soils have very little inherent structure and are mainly bound together by roots. In contrast, mineral soils have superior structures derived from the more cohesive mineral particles in the soil. Peat soils are very vulnerable to physical disturbance because of their soft nature and typically waterlogged condition.

Peatlands are affected in the following ways by fire in increasing order of impact:

- Removal of some vegetation and litter left intact leaving a protective layer.

- Removal of all vegetation with some surface litter left intact leaving a protective layer.

- Removal of vegetation and surface litter which exposes the soil surface potentially leading to greater drying and cracking of the peat. If the removal of vegetation and litter occurs frequently the raw material for organic soil development is lost which can retard soil formation. Ash may be blown or washed away.

- Removal of vegetation, litter and peat to varying depths. Ash may be blown or washed away. The more soil removed the longer it is likely to take for the soil to reform because of greater stresses on plant development. Soils can be burnt to bedrock or underlying mineral substrates.

Evidence for erosion of peat includes exposed substrates, truncated peat profiles, accumulation of organic matter at the change of slope and peat profiles covered by a layer of sand which has been washed downslope (Pemberton 1989). The other major physical impact is complete removal of all seed stock. Seed is unlikely to survive peat fires, which can burn at temperatures of between 300 and 600° C (Frandsen 1991).

If surface organic material is burnt, differential removal can lead to the formation of surface irregularities or small pits which may alter vegetation patterns and creates a hummocky land surface. This has occurred in parts of Tasmania, the Swan Coastal Plain and most likely other peatlands in Australia. Where fire does expose a mineral surface plant establishment is hindered by summer drought which can have serious implications for plants that are adapted to wet conditions.

Estimates in Tasmania suggest up to 3 million m³ (100 000 ha) of organic soil has been lost from blanket bogs due to fire with some profiles having been burnt to bedrock (Pemberton & Cullen 1995). The complex relationship between the fire adapted buttongrass communities which develop on the peatland and the

(potentially) vulnerable soils which occur below need careful land management/conservation consideration. There is a question of whether these communities actually need fire to develop.

Agriculture and Urban Expansion

Some of the greatest impacts on peatlands have occurred to coastal peatlands from drainage for agriculture and settlement. In Victoria and South Australia interdune swale peats and riverine peats have been impacted with the loss of up to 2000 000 ha of peatland. Drainage has resulted in oxidation of the peat and further loss through fire (Taffs 2001).

Montane mires have also suffered from fires where drainage and burning to promote pasture grasses has destroyed peats (Cullen 1995). Peatlands in tropical Australia (Whinam & Hope in prep) are threatened by drainage works and a reduction in groundwater resulting from over-exploitation of artesian water supplies.

Urban expansion in many locations has resulted in the drainage and "in-filling" of peatlands. The exploitation of groundwater resources also provides a direct threat to these ecosystems. Unchecked urban expansion will continue to apply pressure. This is most notable on the Swan Coastal Plain.

Peat Extraction

Removal of peat for horticultural uses has occurred in a wide range of peatland ecosystems across Australia. In comparison to the Northern Hemisphere, where it is also used as a fuel, Australian peat mining operations are reasonably small, but the extent of this countries peatlands does not compare with those of the Northern Hemisphere. In the Northern Hemisphere peat extraction for power plant operation has all but destroyed the blanket bogs in the United Kingdom and Ireland (Lindsay 1995).

Unreserved *Sphagnum* moss peatlands in Tasmania and Victoria have been under considerable pressure for harvesting where attempts have been made at sustainable harvest by removing shallow surface layers of moss (Whinam *et al* 1989). This is not necessarily the case in many other locations such as Western Australia and New South Wales where peat is removed right down to the mineral substrate. This effectively mines out the peatlands, which can take thousands of years to regrow if the right conditions occur. Perhaps one of the best known examples of peatland extraction is Wingecarribbe swamp in New South Wales, which collapsed following extensive mining carrying peat and sediment into the neighbouring Wingecaribee Reservoir (Arachchi & Lambkin 1999).

Climate Change

Peatlands are threatened by global climate change (Charman 2002), but also pose a threat if they are burnt or drained (Intergovernment Panel on Climate Change 2001) as this can lead to large carbon emissions. It is estimated that 500–1000 million tonnes of carbon dioxide was emitted from peatland fires in Indonesia in 1997–1998. Many peatlands are net carbon sinks and all store significant amounts of carbon. It is estimated that worldwide peatlands store up to 550 billion tones of carbon and they store more carbon per unit area than any other ecosystems (Lafleur *et al* 2003). Pastor *et al* (2003) estimate that peatlands contain about one third of the world's soil carbon pool. If, as a consequence of climate change, peatlands stop accumulating and start releasing carbon, as they decompose or are burnt, the threats posed are to the worlds climate and the peatland as well.

Climate change also directly threatens many peatlands due to the reliance of these ecosystems on high humidity, low evaporation and adequate rainfall for their well being. Although these conditions may be enhanced in some parts of the world, which is not necessarily a good thing, there are other parts where peatlands could be stressed by climate change. Australia is one such area.

Increases in temperature across Australia of between 1.0–6.0° C are expected by 2070 (Howden 2003). The CSIRO (2001) has predicted increased rainfall in summer and autumn for most of Australia, but a wetter winter and drier spring, summer, and autumn for south eastern Australia. Peatland ecosystems in south eastern Australia could be under increased pressure as a consequence. Recent investigations in Tasmania indicate that evaporation is greater than precipitation during drier months and that recent extended dry periods and lower water tables have been recorded for blanket bogs in the State (Bridle *et al* 2003). It is unclear whether these peatlands are actively accumulating and there is some indication that they are in decline. Increased drying may well result in an accelerated decline.

Conclusions

Peatlands are unusual ecosystems to find on the second driest continent in the world. Although rare, they have developed in restricted habitats in Australia around the coast, in montane locations, in deflation hollows and, the most peculiar, in the deserts associated with the Great Artesian Basin spring mounds. They have both biotic and abiotic conservation values, which need to be taken into account when considering management and protection requirements.

Some of Australia's peatlands remain in reasonably good condition and although no systematic review of these ecosystems has been conducted, it seems apparent that it is the coastal peatlands which are under considerable pressure from land use change, fire, water extraction and drainage. Other risks include grazing, burning and weed invasion in montane peatlands. The pressure on the inland desert peatlands arises from stock access and broader pressures on the Great Artesian Basin. Deflation hollow peatlands have been impacted by forestry operations and agriculture.

Management and conservation of peatlands needs to include more of the peatland than its physical boundaries given the potential complexities of their hydrological relationships.

There is an urgent need for investigations of the spatial extent of peatlands and an assessment of peatland condition and management requirements in Australia. The land use and development pressures also require

identification and, most importantly, hydrological characteristics and influences on peatland hydrology should be investigated.

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APPENDIX 1

Organosol suborders are defined as follows:

"**Fibric** – Soils in which the *organic materials* are dominated (about 75 % by volume) by *fibric peat*.

Hemic – Soils in which the *organic materials* are dominated by *hemic peat*.

Sapric – Soils in which the *organic materials* are dominated (about 75 % by volume) by *sapric peat*." (Isbell 2002).

Fibric, hemic and sapric peat are further described by Isbell (2002) as follows:

"**Fibric Peat** – Undecomposed or weakly decomposed organic material; plant remains are distinct and identifiable; yields clear to weakly turbid water; no peat escapes between fingers (authors note; when squeezed in the palm of the hand).

Hemic Peat – Moderately to well decomposed organic material; plant remains recognisable but may be rather indistinct and difficult to identify; yields strongly turbid to muddy water; amount of peat escaping between fingers ranges from none up to one-third (authors note; when squeezed in the palm of the hand); residue is pasty.

Sapric Peat – Strongly to completely decomposed organic material; plant remains indistinct to unrecognisable; amounts ranging from half to all escape between fingers (authors note; when squeezed in the palm of the hand); any residue is almost entirely resistant remains such as root fibres and wood."

Organic materials:

"These are plant-derived organic accumulations that are either:

(i)   Saturated with water for long periods or are artificially drained and, excluding live plant tissue, (a) have 18 % or more organic carbon (Wakley-Black x 1.3 or a total combustion method, Rayment and Higginson 1992, Methods 6A1 or 6B2 in Isbell 2002) if the mineral fraction is 60 % or more clay, (b) have 12 % or more organic carbon if the mineral fraction has no clay, or (c) have a proportional content of organic carbon between 12 and 18 % if the clay content of the mineral fraction is between zero and 60 % or

(ii) Saturated with water for no more than a few days and have 205 or more organic carbon." (Isbell 2002)

Loss on ignition

Loss on ignition may be used as an estimate of organic carbon.

APPENDIX 2

Geodiversity can be defined as "The natural range (diversity) of geological (bedrock), geomorphological (landform) and soil features, assemblages, systems and processes. Geodiversity includes evidence for the history of the Earth (evidence of past life, ecosystems and environments) and a range of processes (biological, hydrological and atmospheric) currently on rocks, landforms and soils" (Eberhard 1997).

Geoconservation can be defined as "The identification, and conservation of geological, geomorphological and soil features, assemblages, systems and processes for their intrinsic, ecological or heritage values "(Eberhard 1997).

Wetland sediments and soils on the Swan Coastal Plain, southwestern Australia: types, distribution, susceptibility to combustion, and implications for fire management

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Abstract

The main types of end-member sediments constituting wetland fill on the Swan Coastal Plain are diatomite, calcilutite (carbonate mud), peat, quartz sand, and kaolinite-dominated mud. There is also a range of intermediate sediments formed as mixtures between end-member sediment types, *viz.*, diatomaceous peat, organic matter enriched diatomite, organic matter enriched calcilutite, and various types of muddy sand. Humified equivalents of these sediments and humified basement quartz sand are the main wetland soils. There is a relationship between composition of the sedimentary fill, landscape setting, hydrochemical setting, and wetland type. Channels and wetland flats associated with the Pinjarra Plain bordering the Darling Scarp, or wetlands in the Pinjarra Plain to Bassendean Dunes transition are underlain by extrabasinal sediments, such as sand and kaolinite-dominated mud and muddy sand, reflecting their delivery and sedimentation by fluvial processes. Basin wetlands in the Bassendean Dunes are underlain by intrabasinal peat, diatomaceous peat, and diatomite, and their intermediates, or by soils composed of humic quartz sand (basement sand). Those in the Spearwood Dunes, within a terrain of quartz sand or limestone, are underlain by intrabasinal peat, diatomaceous peat, or calcilutite, often interlayered. Basin wetlands in the Quindalup Dunes are underlain by intrabasinal calcilutite, calcilutaceous sand, and some peat. Climate influences the distribution of the type of the wetland sediments in a south to north latitudinal gradient along the Swan Coastal Plain (*i.e.*, for a given geomorphic setting, peat tends to be more abundant in wetland basins in southern humid environments, and diatomite and calcilutite fills are more abundant in northern semi-arid environments). Climate also influences the temporal variation in material flammability as related to fluctuating or declining water tables. The various wetland sedimentary fills are mineralogic, geochemical and biochemical reservoirs that have varying response to combustion, producing different types of smoke and dust, factors important in designing fire management strategies. Pre-emptive and operational management of fire in wetland sediments and soils should be based on knowledge of their organic carbon content, their mineralogy, geochemistry and biochemistry, their hydrology, the potential of the sediments to combust in relation to annual water table fluctuations and longer term climatic patterns, the extent of flammable material across a wetland, the nature of stratigraphic interlayering along wetland margins, and the distribution of wetland sediment types both across the Swan Coastal Plain and along the climatic gradient of the length of the Swan Coastal Plain.

Keywords: wetland sediments, fire, pyrosediments, wetland hydrology, climate changes, Swan Coastal Plain wetlands

Introduction

Whereas fires in dryland environments consume vegetation and litter (Luke & McArthur 1978; Gill *et al* 1981), and in high temperature combustions may rapidly oxidise and remove humic soils, wetlands with organic matter rich substrates that become dry and flammable in the summer add another dimension to fire management, *i.e.*, how fires are ignited, fuelled and sustained, what remains as combustion residues, and what biochemical, geochemical, and mineralogic species are mobilised into the smoke or remain as ash. In the first instance, for example, while material such as peat may be more flammable than other wetland sediments, the opportunity for its combustion is closely related to the dynamics of the water table. For wetlands of the Swan Coastal Plain, one of the important tools in the management of fires thus is information on the distribution of flammable materials in the wetland systems, and the likelihood that such materials will be ignited. In this context, information on wetland sediments, wetland stratigraphy (*i.e.*, the thickness, sequences and types of wetland sediments and their mineralogy and geochemistry), surficial soils, and hydrology, (*i.e.*, the annual to long-term dynamics of inundation and waterlogging), should form cornerstones to an understanding of fire dynamics in wetlands and the development of strategies for managing fires in these environments.

This paper, as part of the Workshop on Fire Management in Wetlands held in Perth in March 2004, presents information on the types and distribution of

wetland sediments and soils on the Swan Coastal Plain in order to identify those that are organic-rich and susceptible to combustion. As such, the paper describes the following: (1) the types of sediment and soils encountered in wetlands; (2) the stratigraphic fill of these wetlands in a geomorphic and climatic setting; (3) some of the responses of wetland sediments and soils to fire; (4) the various types of sediments and soils in wetlands in relation to their geomorphic setting and occurrence in natural wetland groups (consanguineous suites) across the Swan Coastal Plain and along a south to north climate gradient; and (5) the role of short-term or long-term groundwater fluctuations as factors in producing dry, flammable organic-rich sediments and soils that will be susceptible to combustion.

Information in this paper is drawn from the study of wetlands and sediments in consanguineous suites across the Swan Coastal Plain (Semeniuk 1988), the description of sediments, soils and stratigraphy in wetland basins across the Swan Coastal Plain (Semeniuk & Semeniuk 2004, 2005a,b), the detailed study of the stratigraphy, hydrology, vegetation and history of the Becher Suite wetlands (Semeniuk 2005), the climate patterns in coastal Western Australia (Semeniuk 1995a), and on R&D data collected over 30 years on the sediments, wetland sedimentary and diagenetic mineralogy, geochemistry, wetland stratigraphy and wetland hydrology by the V & C Semeniuk Research Group (Semeniuk & Semeniuk, 2005c).

From a stratigraphic and hydrologic perspective, the ignition and ongoing combustion of flammable materials in wetlands spatially and temporally are related to four factors: 1. the type and state of combustible materials resident in wetlands (Fig. 1); 2. the stratigraphic distribution of flammable materials across a wetland and down the stratigraphic profile; 3. the distribution of such materials, which is related to geomorphic setting and climate setting; and 4. the seasonal patterns, or longer term climatic patterns that result in potentially flammable materials drying out.

Materials and methods

A wide-ranging sediment/soil sampling programme was undertaken by Semeniuk & Semeniuk (2004) at the surface and in the stratigraphic sequence of 143 wetlands, from Bunbury to the Moore River, across the width and along the length of the central Swan Coastal Plain in the different geomorphic, hydrologic and hydrochemical settings, in order to fully capture potential variability in these materials. The details of methods used in the study of wetland sediment/soils are provided by Semeniuk & Semeniuk (2004, 2005a), but a summary is provided here.

In the laboratory, the samples of sediment/soils were described and analysed using various levels of detail to provide a comprehensive view of the variety of wetland sediment and soil types on the Swan Coastal Plain (Semeniuk & Semeniuk 2004, 2005a): stereomicroscope and a light transmitting microscopy; chemical analyses for various alkali metals, heavy metals, and S; determination of carbonate by acid digestion and high temperature combustion; C determination by combustion; selected analyses of some 50 samples at the CSIRO laboratories by Scanning Electron Microscope (SEM), supplemented by use of Back-scattered Electron Emissions (BSE), Energy Dispersive Spectroscopy (EDS), and XRD; routine spot analyses of numerous (5–15) particles within each SEM field of view, using EDS, which allowed determination of relative element content of individual particles and identification of diatoms, very fine and ultra-fine-grained diatom fragments, sponge spicules, invertebrate skeletons/tests and fragments, quartz silt, mud-sized phyllosilicate minerals, organic carbon, plant detritus, calcite, and framboidal pyrite, and in the ash, alkaline metal salts.

The effects of fire on sediment/soils were studied using natural materials in the field, and using laboratory procedures. In the first instance, during the 30 years of monitoring and studying wetlands stratigraphically on the Swan Coastal Plain and elsewhere, numerous wetlands through natural or anthropogenic agencies had been burnt during late summer. The water tables in these wetlands at the time of the fires generally were low, and surface sediments and soils were invariably dry. Forty seven of these had been sampled for surface sediments and eight had been sampled for soils before the combustion event, and had been analysed in terms of organic matter, diatoms, and carbonate mud as part of a regional study (Semeniuk & Semeniuk 2004). The responses of the surface materials to these fires were observed (*i.e.*, whether or not they had combusted), and the nature of the post-combustion residue or ash remaining analysed texturally, mineralogically, and in terms of elemental composition, and thus could be compared with pre-combustion sediments. In relation to laboratory procedures, a range of experiments were conducted to determine the effects of fire on particular grain types and minerals in various materials (*e.g.*, peat, spongolitic peat, peaty diatomite, peaty calcilutite, and other organic rich sediments, as well as diatomite, sponge spicules, pyrite, a pyrite/diatomite powder mix, and wood). Separate sample batches of these materials were combusted for 1 hour and for 2 hours at 250° C, 500° C, 750° C, and 1000° C to ascertain in the laboratory the textural and mineralogic transformations that may occur with the high temperatures achieved during natural combustion in wildfires. For the sediments, the pre-combustion and post-combustion samples were digested in perchloric acid and nitric acid, and analysed for Na, K, Ca, Mg, Fe, As, Pb, and S by Atomic Absorption Spectroscopy or ICP-MS, and selected pre-combustion and post-combustion samples were analysed by XRD. Pre-combustion and post-combustion samples were also examined as grain-mounts under petrographic microscope. The alkaline metal content of vegetation was determined by combusting various plant species, digesting the ash in perchloric acid and nitric acid, and analysing the liquor for Na, K, Mg, and Ca by Atomic Absorption Spectroscopy or ICP-MS (Semeniuk 2005).

Terminology

Because of some confusion and free substitution in the literature between the terms "sediment" and "soil", Semeniuk & Semeniuk (2004) defined a range of terms in relation to wetland-filling materials. "Sediment" refers to
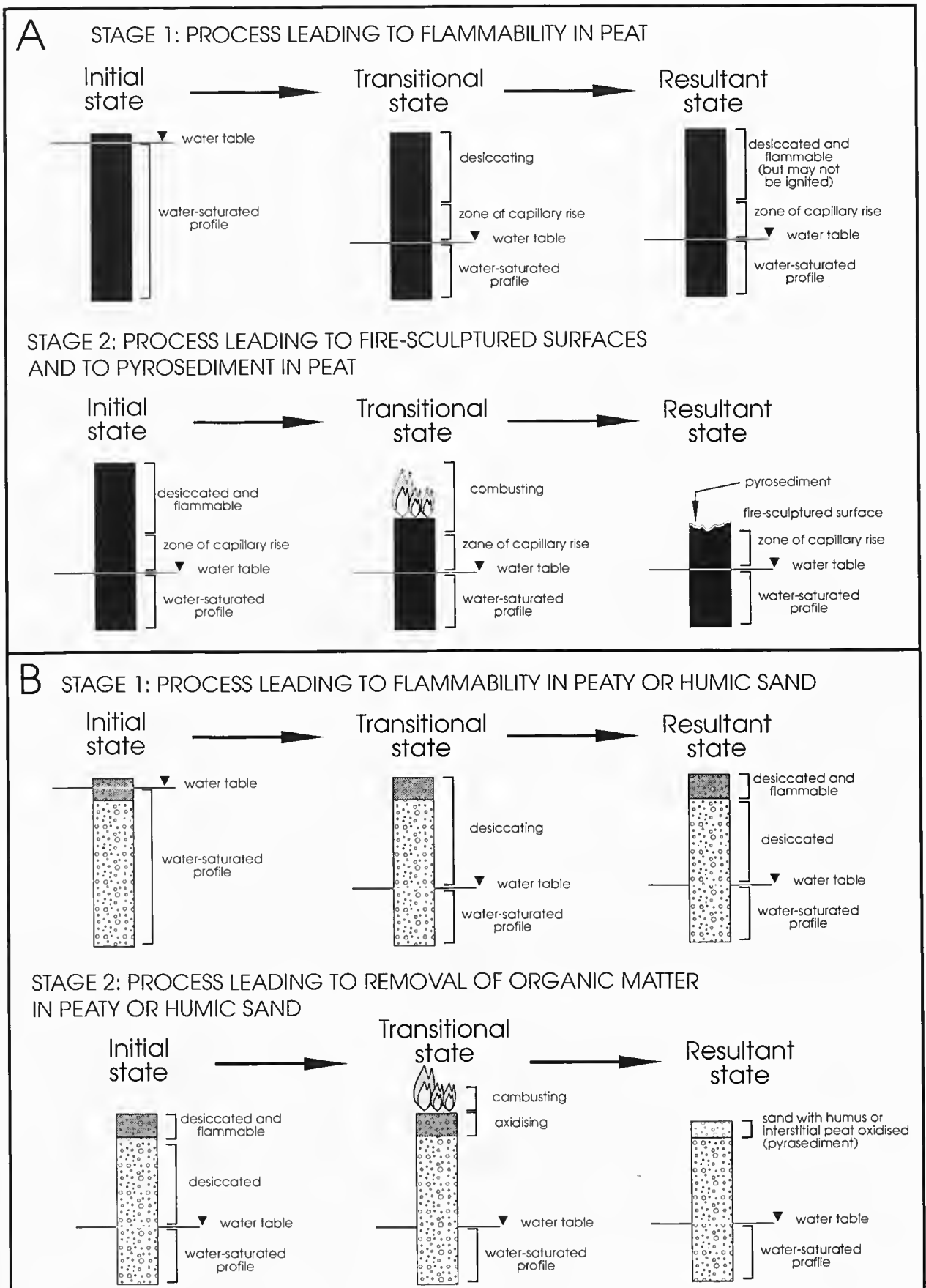
Figure 1. Processes leading to flammability of combustion-susceptible sediments and soils. In all these idealised stratigraphic columns, the depth of the profile is 2 m, and in general, the zone of capillary rise is up to 30 cm above the water table. A. Stage 1 involves falling water level and water table, leading to desiccation and a state of flammability (though not necessarily combustion). Stage 2 involves combustion of flammable material, leading to fire-sculpturing of the surface, and development of pyrosediments. B. Similar processes, but with a humus rich quartzose sand soil, or peaty sand.

accretionary and infiltrational material formed within the wetland (autochthonous, intrabasinal), or transported into the wetland (allochthonous, extrabasinal). Thus, peat and calcilutite as accretionary materials are types of wetland sediment, formed intrabasinally. "Sedimentary fill" refers to the total aggregate of sediments that have accumulated in a wetland basin upwards from the floor of the original ancestral basin. "Stratigraphic" and "stratigraphy" refer to the accumulated sequence of sediments. "Diagenetic" refers to the physical, biological, and chemical processes, acting alone or in concert, that overprint sediments after accumulation, and products resulting from these processes, e.g., precipitation of pyrite and carbonate cementation. Processes of diagenesis can overlap with pedogenesis. "Soil" refers to the altered material near or at the surface of any pre-existing sediment or rock body that has been biologically, chemically, or physically (pedogenically) modified under extant conditions, e.g., the weathering and humification of the surface layer of sand results in a surficial soil (Fig. 1 of Semeniuk & Semeniuk 2004). Soils that are buried, or that have formed under past climatic or hydrologic conditions, and therefore not extant, are palaeosols.

Wetland sediments are the primary (accretionary or infiltrational) accumulates within a wetland basin. Wetland soils are the surface and near-surface alteration either of these sedimentary materials, or of the parent "basement" material. Two examples are used to illustrate the principles that soils may be developed on wetland sediment or on basement materials. Whereas calcilutite fill within a wetland basin is accretionary intrabasinal sediment, the near-surface 10 cm thick grey calcilutite layer, with humified root-structured material, is the wetland soil. A wetland underlain only by basement quartz sand, e.g., the Bassendean Sand (Playford & Low 1972), has no wetland sediment, thus any near-surface 10 cm thick grey sandy layer of humified root-structured sand is the wetland soil.

Pyrosediments, a term coined by Semeniuk & Semeniuk (2004), are secondary sediments, such as residues of diatomite, calcilutite, and quartz sand, formed as a result of the combustion of sedimentary materials. Various aspects of wetland pyrosediments and their diagnostic signatures of wetland sedimentary particles are described and discussed in Semeniuk & Semeniuk (2005a).

In this paper, following Semeniuk & Semeniuk (2004), the term "organic matter" is used to refer to the range of materials of various particle sizes that are derived mainly from plants. Organic matter ranges from relatively fresh plant material, to particles in various stages of decomposition (structural and biochemical breakdown, mediated by microbiological and fungal processes), to elemental carbon. The term "organic matter" is not used to refer to skeletal remains of invertebrate fauna, the calcareous products of disintegrated charophytes, or to the frustules of diatoms, though these particle types are produced by organic processes.

We separate three terms in the description of fire in wetland sediments, or the effect of fire on wetland soils: (1) *combustion*, a general term for the exothermic rapidly oxidising chemical reaction of materials which once ignited is self-sustaining and usually produces a flame; (2) *flammable*, referring to the property of materials that

combust, often resulting in flames; and (3) in this paper, *rapid oxidation*, usually of soil materials, driven by the heat of fire in the overlying vegetation, and referring to the removal of soil carbon or organic matter as CO_2 without combustion or flammability of the material.

Regional setting and consanguineous wetland suites

The Swan Coastal Plain is the Quaternary surface of the Perth Basin (Playford et al 1976). The Plain comprises distinct large-scale landforms arranged subparallel to the Darling Scarp, or to the coast, except where they are associated with major rivers. These landforms correspond to the main sedimentary formations in the region (Woolnough 1920; McArthur & Bettenay 1960; Playford et al 1976; McArthur & Bartle 1980a,b; Semeniuk & Glassford 1987, 1989; Semeniuk 1988; Semeniuk et al 1989; Geological Survey 1990; Semeniuk 1995b). The units from east to west are (Fig. 2A):

- Pinjarra Plain: flat to gently undulating alluvial fans fronting the Darling Scarp and Darling Plateau (underlain by sand, laterite, and the Precambrian rocks), as well as floodplains and various sized channels; underlain by the Guildford Formation (clay, laterite, sand, muddy sand);

- Bassendean Dunes: undulating terrain of low degraded dunes (varying in relative relief from 20 m to almost flat), and interdune flats and basins; underlain by the Bassendean Sand (quartz sand) of Pleistocene age;

- Spearwood Dunes and Yalgorup Plain: large-scale, linear, near-continuous subparallel ridges (c 60m relief) and intervening narrow and steep-sided depressions, or of narrow plains; underlain by Pleistocene limestone (aeolianite and marine limestone) blanketed by quartz sand;

- Quindalup Dunes: Holocene coastal quartzo-calcareous sand dunes, beach ridge plains, tombolos and cuspate forelands.

A wide range of wetland types occurs on the Swan Coastal Plain, from basins (lakes, sumplands, and damplands) to flats (floodplains and palusplains) to channels (rivers and creeks), varying in size, shape, water characteristics, stratigraphy and vegetation (Semeniuk 1987, 1988; Semeniuk et al 1990). For instance, dependent on setting, wetland basins can range from large linear lakes to small round to irregular seasonally damp basins; from fresh water to hyposaline (brackish) to saline (Semeniuk 1987); from surface-water to groundwater recharged; their vegetation cover can vary from herbland to forest (Semeniuk et al 1990). All these attributes are influenced by regional features such as geology, geomorphology, soils, climate and hydrology, and local physical/chemical processes such as aeolian processes, groundwater flow, and karstification.

The variety of wetlands formed on the Swan Coastal Plain can be aggregated into natural groupings, *i.e.*, consanguineous suites (Semeniuk 1988), with each suite having its own variety of wetland types in terms of size, shape, water quality, substrates, and maintenance processes. Wetland suites are strongly related to
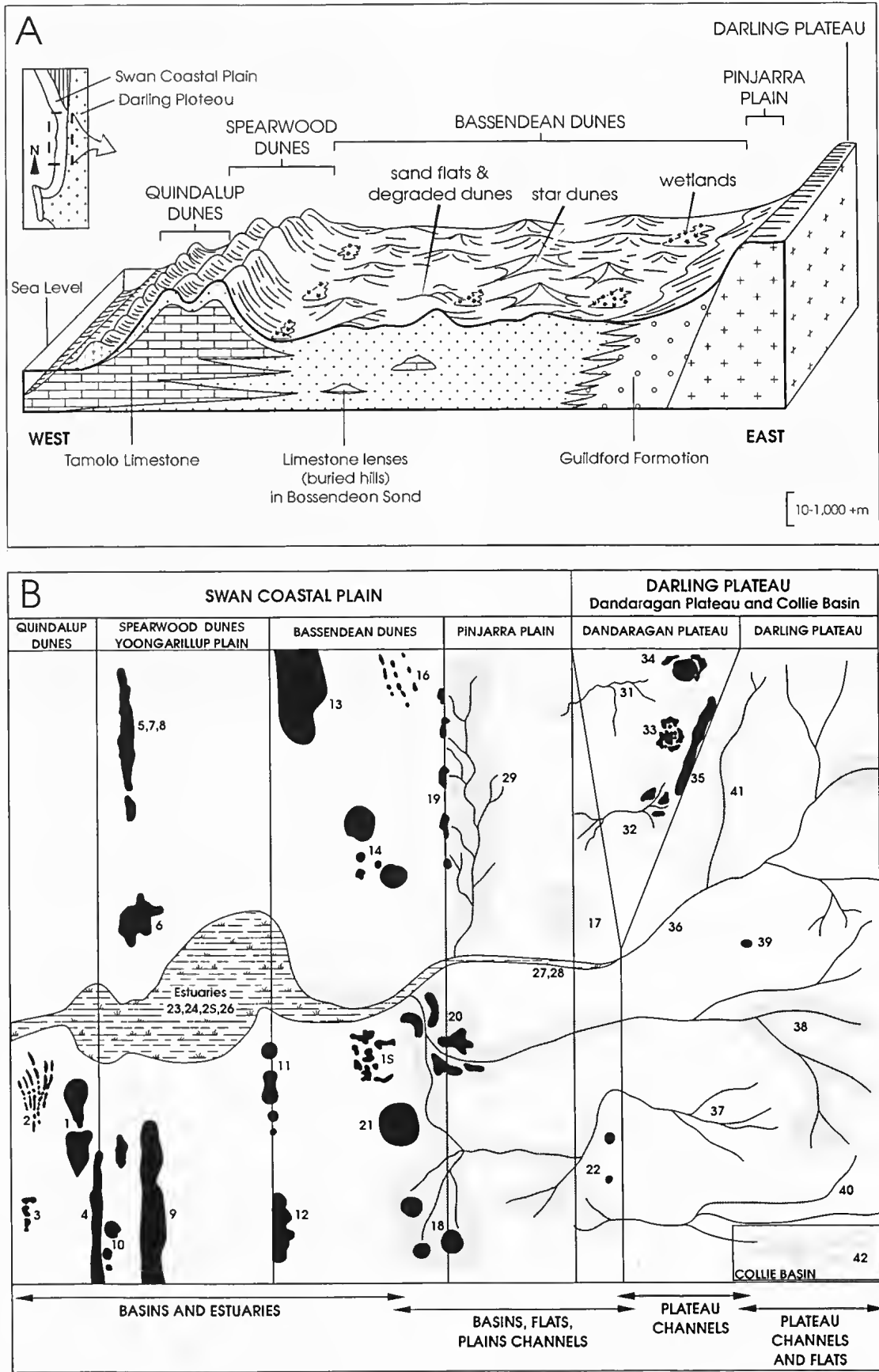
Figure 2. A: Idealised block diagram showing geomorphic units of the Swan Coastal Plain, their sub-parallelism to the Darling Scarp and the coast, their gross surface features, and their stratigraphy, with some details of landscape (after Semeniuk & Glassford 1989). B: Idealised map showing the variety and distribution of consanguineous wetlands (from Semeniuk 1988), i.e., the natural wetland groupings or suites in the Darling Plateau and Swan Coastal Plain centred on the Moore River to Bunbury region. In this region there are 42 such groups each related to geomorphic setting, or interfaces between geomorphic units (for explanation of numbering of the consanguineous wetland suites, see Semeniuk 1988).

geomorphic setting, or to the interfaces between the main geomorphic units. An idealised diagram of the range of consanguineous suites across the central Swan Coastal Plain is shown in Figure 2B. Each individual or site-specific wetland, and wetland suite, is the culmination of broader Quaternary palaeoenvironmental as well as more modern processes such as geomorphic and sedimentologic processes, vegetation influences, and fire.

Wetland types and the origin of wetlands within a consanguineous suite tend to be similar because of the similarity of physical setting and causative factors, *i.e.*, geomorphology, geomorphic and sedimentologic processes and developmental history, climate, and hydrology. As such, for instance, within the Bassendean Dunes, wetlands set in geomorphically degraded dune terrain appear as a dappled pattern of irregular small wetland basins; within the beachridge setting of the Quindalup Dunes, there are linear patterns of small, oval to linear wetlands reflective of a setting in inter-beachridge swales; and along the interface between the Spearwood Dunes and Bassendean Dunes there are large, round wetlands set in a chain, reflecting the long term hydrological setting between these two geomorphic units (Semeniuk 1988). If concurrently there exists a pattern of wetland types, hydrology, hydrochemistry, and foundation materials, as related to geomorphic setting, similar suites of sedimentary fill also will be developed. Sedimentary fills within wetlands will therefore have a distinct geographic distribution. For example, wetlands residing in carbonate-enriched groundwaters will develop calcareous sediments, and those residing in carbonate-depauperate, silica-enriched groundwaters may have silica-enriched sediments. Thus geomorphic setting, hydrological and hydrochemical setting, expressed within a consanguineous suite will determine to a large extent the type of sediments and soils that will develop within a wetland (Semeniuk 1988).

Wetland sediments and soils, their general flammability, and products of combustion

Wetland sediments and soils

The particles that comprise wetland sediments and soils vary from mud-sized, to gravel-sized. Their composition may be organic matter, biogenic silica (diatoms, sponge spicules, and phytoliths), carbonate minerals, quartz, feldspar, mud-sized phyllosilicate minerals, or gypsum. Diagenetic products within wetland sediments include carbonate cements, silica cements, ferricrete, and the formation of sulphides (especially sulphides such as pyrites, marcasite, and arsenopyrites). Based on composition and texture, Semeniuk & Semeniuk (2004) recognised ten main end-member sediment types in wetlands of the Spearwood Dunes, Bassendean Dunes and Pinjarra Plain on the Swan Coastal Plain, focused only in the central Swan Coastal Plain mainly between Moore River and Bunbury; they are: 1. peat; 2. peat intraclast gravel and sand; 3. calcilutite; 4. carbonate skeletal gravel and sand; 5. carbonate intraclast gravel and sand; 6. diatomite; 7. diatomite intraclast gravel and sand; 8. kaolinitic mud; 9. quartz sand; and 10. quartz silt. However, for completeness of this paper, the full range of the wetland

sediments of the Quindalup Dunes are included here (Semeniuk 1988, 2005). Basins in the Quindalup Dunes contain, as end-member sediments, calcilutite and peat (as above) and additionally quartzo-calcareous sand of aeolian origin and locally stromatolitic boundstone. In total therefore, while Semeniuk & Semeniuk (2004) list 10 end-member wetland sediment types for the central Swan Coastal Plain, for purposes of this paper, incorporating the geomorphic settings of Quindalup Dunes, Spearwood Dunes, Bassendean Dunes and Pinjarra Plain, there are 12 *end-member* wetland sediment types.

Mixtures of these end-member sediment types, contributions to peat and diatomite from sponge spicules and phytoliths, and mixtures between the primary sediments and quartz sand (that forms the basement or the margins to the wetland deposits) also occur (Semeniuk & Semeniuk 2004), resulting in spongolitic peat, diatomaceous peat, calcilutaceous peat, spongolitic diatomite, peaty sand, and muddy sand (calcilutaceous muddy sand, diatomaceous muddy sand, and kaolinitic muddy sand), amongst others. For purposes of this paper, a total of 21 common wetland sediments are described, *i.e.*, 12 end-member sediments and 9 sediment types formed by mixing of the end-member sediment types. These sediments, the mixtures between them, and their general flammability are described in Table 1. SEM photomicrographs of selected standard sediments are illustrated in Figure 3.

Organic, diatomaceous, and calcilutaceous fine-grained wetland sediments were classified by Semeniuk & Semeniuk (2004) using a ternary diagram (Fig. 4A). In this context, peat *sensu stricto* (*i.e.*, sediment with > 75% organic matter) is only a moderately common wetland sediment on the Swan Coastal Plain. Many of the dark grey sediments, high in organic matter (*i.e.*, 50–75% organic matter), superficially resembling peat *sensu stricto*, have significant content of diatoms or carbonate mud, and while belonging to the broad family of "peat" or "peaty" sediments, are termed "diatomaceous peat" and "calcilutaceous peat". Other fine grained dark grey sediments also superficially resembling peat, or appearing to be organic-enriched sediment, often have significant content of metal sulphides, particularly pyrite, that imparts a dark grey tone to the sediment. Thus, sediments that are organic-matter-rich, and not merely dark grey, and that are most susceptible to combustion, while belonging to the family of "peats" or "peaty sediments", are subdivided into peat (*sensu stricto*), diatomaceous peat and calcilutaceous peat.

Soils underlying wetlands are the organic-rich (humified) surface layer and root-structured zones most commonly developed on the primary wetland sediments listed above, but also are formed on basement quartz sand (Semeniuk & Semeniuk 2004). Where transformed to soil at the surface, depending on their content of organic matter, and particularly if they have concentrations of shallow root mats, all wetland sediment types and basement quartz sand may have some degree of flammability, or have the potential to lose their organic matter content through rapid oxidation under fire conditions (*e.g.*, humic quartz sand under damplands in the Bassendean Dunes may be oxidised to quartz sand biogenic sediments based on their content of organic
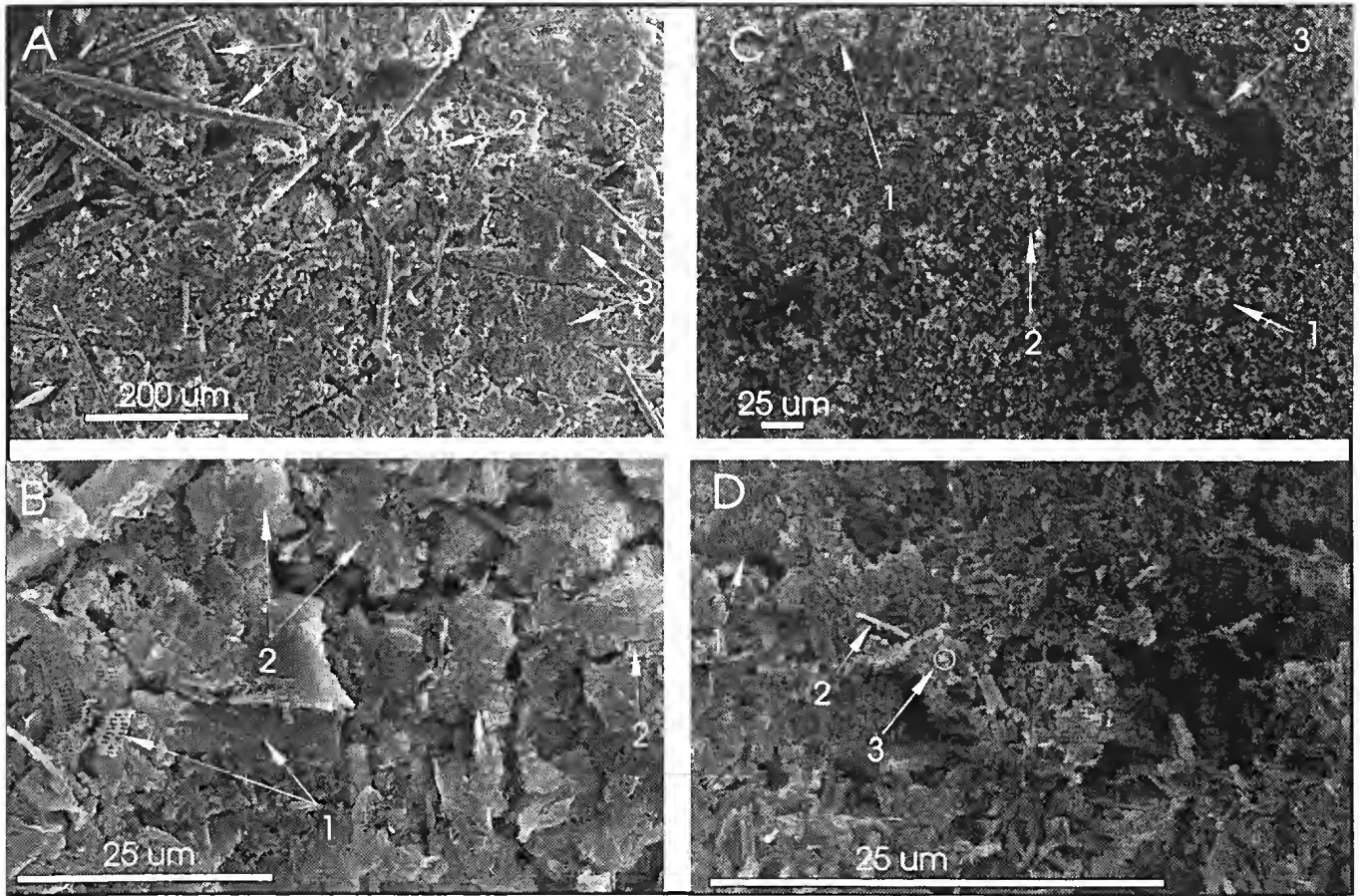
Figure 3. SEM photomicrographs of some wetland sediments. A. Diatomaceous peat showing abundance of whole and fragmented sponge spicules, 200–250 µm in size (arrow 1), scattered diatom fragments (arrow 2), and the fine-grained organic matter that dominates the sediment, here showing cracking by desiccation (arrow 3), as a result of carbon-coating under vacuum in the SEM process. B. Diatomaceous peat showing (1) typical fragments of diatom frustules, and (2) fine-grained plant detritus with layered internal structure. C. Calcilutite with carbonate grains showing progressive disintegration of *Chara*; larger fragments (1), 25–30 µm in size, disaggregated into smaller crystals (2), 1–4 µm in size; invertebrate skeletal fragments are scattered in the sediment (3). D. Diatomite showing progressive fragmentation of frustules from relatively large fragments (1), 5 µm in size, that exhibit wall structure, to nearly fully disaggregated frustules (2), to completely disaggregated frustules (3) < 1 µm in size.

of root mats may localise horizon-specific subsurface combustion zones).

Pyrogenic effects on wetland sediment/soils and particles

During the 30 years of monitoring and studying wetlands stratigraphically and sedimentologically, we have observed numerous wetlands that had been burnt during late summer, both on the Swan Coastal Plain and in other wetland regions of Western Australia. The response of the surface sediments and soils to these fires were noted, *i.e.*, whether or not they combusted. Forty seven of these wetlands fortuitously had been sampled for surface sediments and eight had been sampled for soils in advance of a given fire.

Three stratigraphic situations determined the response of the surface material to the fire (Fig. 5):

1. surface materials consisted of organic-matter-rich sediment such as peat or diatomaceous peat, and combustion consumed the flammable material to the level of the zone of capillary rise;

2. surface materials consisted of sediments that were non-flammable, *e.g.*, diatomite, but the shallow

subsurface layer consisted of an organic-matter-rich root mat (derived, for instance, from *Kunzea ericifolia*, or from *Melaleuca* spp), which preferentially combusted, while underlying and overlying non-flammable layers of sediment, while not combusting, manifest structural, textural and compositional pyrogenic changes; often the root mat has developed because of the relatively impervious nature of the underlying fine grained wetland sediments; in this context, copses of shrubs and trees, therefore, would localise near-surface to subsurface combustion, depending on the depth of the root mat layer and its accessibility to the fire;

3. surface material is a soil with strong humic content or organic matter enriched zone developed on quartz sand, or calcilutite, both of which were not flammable; during a fire, while the quartz sand, or calcilutite remained non-flammable, the organic content of the soil was removed by rapid oxidation, locally resulting in a volume change in the material.

A ternary diagram classifying the fine-grained biogenic sediments based on their content of organic

Table 1

Description of wetland sediments (summarised from Semeniuk & Semeniuk 2004), ordered in terms of potential flammability

Sediment type	Description[1]	Origin	Potential flammability[2]
peat	black to grey, brown, homogeneous to root-structured to finely laminated, mainly fine-grained organic matter, with root fibres, plant detritus and scattered sand, and freshwater snails (or fragments); some peats with branches, twigs, and logs; often containing diatoms, phytoliths, and sponge spicules; organic matter content > 75%	derives from plant detritus, under acidic and anaerobic conditions in wetlands in all geomorphic systems; different types of peat are generated, in terms of their biochemical, geochemical, mineralogic, and sedimentary attributes, by different vegetation assemblages, viz., Typha peat, Baumea articulata peat, Melaleuca peat, and their sedimentary setting	high
peat intraclast gravel and sand	black to grey, breccioid to conglomeratic, grading to sand-sized clasts of peat, or alternating layers of breccia, conglomerate, and sand-sized fragments of indurated peat; may be texturally layered, and root-structured	drying, cracking, heat induration, fragmentation and reworking of peat in wetlands of Bassendean Dunes	high
diatomaceous peat (and spongolitic diatomaceous peat)	peat as above, but with 50–75% organic matter content, and with significant diatom content, and often significant sponge spicule content	diatoms (and sponge spicules) mixed with plant detritus	high
peaty sand	quartz sand as above, but with fine-grained interstitial material with > 75% organic matter	organic mud mixed into sand at margins or at base of wetland	medium to low
calcilutaceous peat	peat as above, but with 50–75% organic matter content, and with significant carbonate mud content	charophytes and invertebrate skeletons comminuted to mud size, mixed with plant detritus	low to nil[3]
organic matter enriched calcilutite	grey to brown homogeneous calcilutite, as above, but with 25–50% content of organic matter	calcilutite as above, but mixed with organic matter derived from plant detritus	nil
organic matter enriched diatomite	grey to brown homogeneous diatomite, as above, but with 25–50% content of organic matter	diatomite as above, but mixed with organic matter derived from plant detritus	nil
calcilutite	cream to pink to grey homogeneous, laminated, burrow-mottled, root-structured, bioturbated, or colour mottled; consists dominantly of clay-sized carbonate particles; mainly calcite, with minor Mg-calcite, aragonite and dolomite, or locally dominantly dolomite; with freshwater snails or fragments	disintegrated charophytes in wetlands of the Quindalup Dunes and Spearwood Dunes; uncommon in the Bassendean Dunes	nil
carbonate skeletal gravel and sand	cream to grey, homogeneous to layered; very coarse to medium sand; consists of whole and fragmented skeletons of molluscs	commonly as layers in peat, deriving from local invertebrate fauna in wetlands of Quindalup Dunes and Spearwood Dunes	nil
carbonate intraclast gravel and sand	cream to grey, structurally homogeneous to layered, with local vesicular to fenestral structures; consists of medium, coarse to very coarse intraclasts of calcilutite or cemented aggregates of carbonate sand	cementation (induration), fragmentation and reworking of carbonate mud and sand in wetlands of Quindalup Dunes and Spearwood Dunes	nil
diatomite (and spongolitic diatomite)	light grey, locally dark grey in humus-rich upper layers, homogeneous to root-structured at the surface and laminated at depth; consists of silt-sized to clay-sized diatom tests and particles (and sponge spicules)	accumulation of diatoms (and sponge spicules) and their fragments in wetlands of Bassendean Dunes	nil
diatomite intraclast gravel and sand	light grey, rounded fine gravel- to sand-sized clasts of diatomite	drying/cracking, fragmentation, and reworking of diatomite along margins of wetlands	nil

Table 1 (cont.)

Sediment type	Description[1]	Origin	Potential flammability[2]
kaolinitic mud[4]	white, orange, dark brown, dark grey to black, homogeneous to root-structured, mostly mud-sized particles with scattered sand; kaolinitic mud is mainly kaolinite, but locally some montmorillonite and sericite; diatoms, sponge spicules and phytoliths are also present	fluvial or aeolian input into wetland, or translocated by groundwater movement in wetlands of Bassendean Dunes and Pinjarra Plain derives from wetland margins	nil
quartz sand[5]	white, light grey to dark grey sand, homogeneous to bioturbated to root-structured; locally with wispy lamination, or with vesicular structure; quartz, with minor feldspar	in wetlands of Bassendean Dunes and Spearwood Dunes	nil
quartzo-calcareous sand	white, light grey to dark grey sand, homogeneous to bioturbated to root-structured; consists of quartz, carbonate grains	derives from the wetland margins in wetlands of Quindalup Dunes	nil
quartz silt	cream to light grey, and structurally homogeneous to root-structured, silt-sized and some clay-sized silica particles, with scattered quartz sand; diatoms, sponge spicules and phytoliths are also present	derives from fluvial groundwater, and aeolian input into wetlands of Bassendean Dunes and Pinjarra Plain	nil
calcilutaceous muddy sand	quartz sand as above, but with interstitial carbonate mud	carbonate mud mixed into sand at margins or at base of wetland	nil
diatomaceous muddy sand	quartz sand as above, but with interstitial diatom mud	diatom mud mixed into sand at margins or at base of wetland	nil
kaolinitic muddy sand	quartz sand as above, but with interstitial mud-sized phyllosilicate mineral particles and quartz silt	mud-sized phyllosilicate mineral particles mixed into sand at margins or at base of wetland	nil
stromatolitic boundstone[6]	laminated, clotted, cemented columns and ellipsoids of cryptalgal (or microbialite[6] of Burne & Moore 1987) deposits composed of skeletal, pelletal and intraclast grainstone	trapping/binding of particles by algae and other biota, and inorganic to biomediated carbonate precipitation in some wetlands in the Quindalup Dunes under saline conditions	nil

[1] there also are a range of diagenetic products that form in wetland sediments (Semeniuk & Semeniuk 2004); these include carbonate cements and nodules, micro-etched surfaces (indicating dissolution) on biogenic silica, the bio-mediated precipitates of FeS_2 as framboidal pyrite, the sulphides of heavy metals and metalloids; these diagenetic products are not described in detail here.

[2] the assessment of potential flammability relates to whether or not sediments have been enriched enough in organic matter; clearly, the minerals calcite (the main constituent of calcilutite), biogenic silica, kaolinite, and quartz are not combustible (hence "nil" flammability); where the sediment has been humified or "organic matter enriched", the potential flammability is assessed as possible but "negligible"; assessment of flammability of the sediments in this Table also is based on the empirical evidence presented in Figure 4.

[3] though the field evidence suggests that calcilutaceous peat is not flammable, the data are limited, hence the sediment is assessed here as low to nil flammability to cover the possibility that some calcilutaceous peat, with coarse silt-sized carbonate particles rather than clay-sized or fine silt-sized carbonate particles, and with high content of organic matter, under an intense fire will combust.

[4] the sediments formed as mixtures between kaolinitic mud and the biogenic muds of peat, diatomite, and calcilutite (Semeniuk & Semeniuk 2004) are not common sediments (the most common of this suite being organic matter-enriched kaolinitic mud, diatomaceous kaolinitic mud, and organic matter-enriched diatomaceous kaolinitic mud).

[5] quartz sand in this context is not the parent "basement" sand, but extrabasinal, transported *into* the wetland basin.

[6] the term "stromatolitic boundstone" is after Dunham (1962); "microbialite" is the term coined by Burne & Moore (1987) for a range of cemented emergent organo-sedimentary structures that include stromatolitic algal boundstone.

matter, diatoms and carbonate mud is provided by Semeniuk & Semeniuk (2004). As mentioned earlier, samples of surface sediments from 47 wetlands that had experienced fire had been analysed as to their particle composition as part of a regional study (Semeniuk & Semeniuk 2004) prior to the fires, and hence these data and the observations on the responses of the wetlands to the fire could be used to explore in a preliminary manner the relation between flammability and sediment type. The data on sediment composition and the observations on the flammability of the sediments underlying these

wetlands are superimposed on the ternary classification diagram (Fig. 4B). The data provided insight into which sediment types were flammable, and with sampling after the fire event, what changes had been effected by the fire.

While organic-matter-enriched sediments clearly are flammable, the presence of $CaCO_3$ appears to raise the threshold at which flammability will occur. That is, while diatomaceous peat with content of organic matter > 60–65% is flammable, calcilutaceous peat needs to have organic matter > 75–80% to be flammable. $CaCO_3$ is
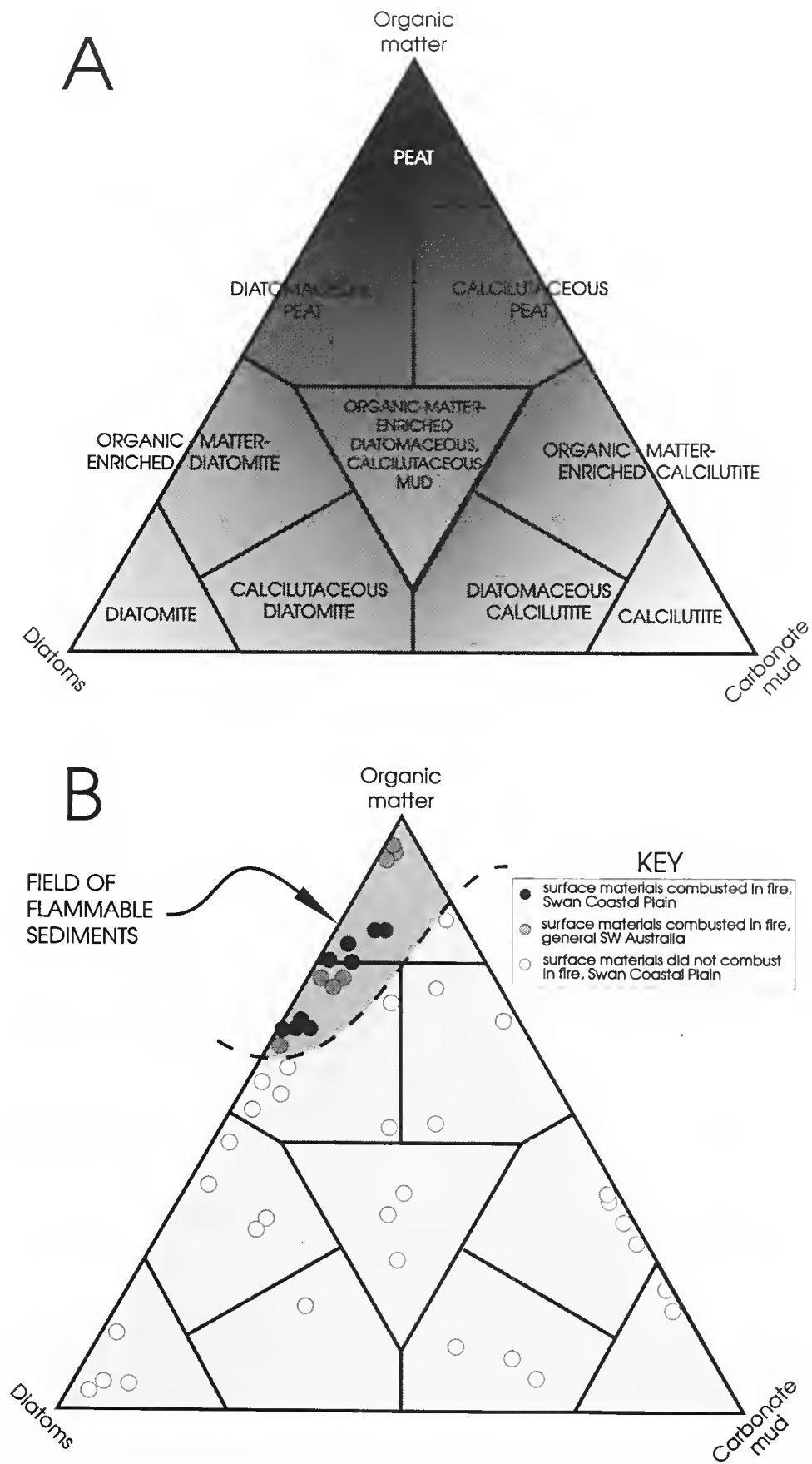
Figure 4. A. Ternary diagram illustrating the categories and nomenclature proposed by Semeniuk & Semeniuk (2004) for fine-grained sediment types that occur as end-members or as mixtures involving organic matter, diatoms, and carbonate mud. B. Superimposed on this ternary diagram are the data on sediment composition of the 47 wetlands that had been involved in bushfires, observations as to whether the sediments had combusted when they were dry at the end of summer, and the tentative boundary between flammable and non-flammable substrates.

A ORGANIC-RICH SEDIMENTS (SUCH AS PEAT) AND THEIR REMOVAL BY COMBUSTION

combusting

peat

fire-sculptured surface

B ORGANIC-RICH ROOT MAT LAYERS, AND THEIR REMOVAL BY COMBUSTION

soil on diatomite

root mat, or organic-matter rich layer in the root mat zone

removal of soil by rapid oxidation

subsurface combustion of root mat, or organic-matter rich layer in the root mat zone = removal of root mat zone

collapse of surface organic-matter depleted sediment into zone where root mat has been removed

diatomite

C ORGANIC RICH SOILS, AND THEIR RAPID OXIDATION (REMOVAL) BY FIRE

soil, or interstitial peat

removal by rapid oxidation

sand with humus or interstitial peat oxidised (pyrosediment)

quartz sand

Figure 5. Three stratigraphic profiles that respond differently in their surface, near-surface, and shallow subsurface materials to fire. A. Peat, wholly flammable in its profile down to the zone of capillary rise. B. Subsurface or near-surface root mat zone with flammable root mat or flammable organic-rich layer. C. Humic soil (organic matter enriched quartz sand), not flammable but loses its organic matter through rapid oxidation during a fire.

known to be a fire retardant (Kroschwitz & Howe-Grant 1992), and the information in Figure 4B indicates that it also plays this role as fine-grained particles in organic-matter-rich sediments. The transformation of $CaCO_3$ into CaO and CO_2, is endothermic, and it would appear that fine-grained $CaCO_3$ in organic-rich sediments absorbs heat from any exothermic reactions triggered by fire, essentially arresting combustion (though not necessarily rapid oxidation) of the organic matter. Release of CO_2 by the chemical breakdown of $CaCO_3$, effectively smothering particle ignition, also may be occurring at fine particle scale, *i.e.*, particle-scale heterogeneity in calorific value of organic material, may result in temperatures sufficient to promote very local micron-scale breakdown of $CaCO_3$ to CaO.

Data on the organic matter content of root mat and organic-matter-enriched layers associated with root mats in three diatomite filled damplands and in one calcilutite-filled sumpland, and data on organic-matter-enriched soils developed on quartz sand underlying four damplands, were obtained prior to bushfires occurring in these wetlands. The root mats and the organic-matter-enriched layers associated with root mats were 5–10 cm thick, containing 22–90% organic matter. The soils generally are up to 10 cm thick, containing 2–3% organic matter. The root mat zones and the soils were resampled after the fires to determine the change in content of organic matter (if any). For two of the fires (in wetland A and wetland C in Melaleuca Park), the root mats were still smouldering in the subsurface several days after the main blaze had self-extinguished. After a fire, the content of organic matter in root mat zones was markedly reduced (Table 2). Also, with the removal of the organic matter, the fire significantly altered the substrate microtopography of root mat zones, e.g., causing excavation of the surface, and/or collapse of the overlying layers into the zone where there had been removal of the flammable material or the material that had been rapidly

Table 2

Comparison between pre-fire and post-fire content of organic matter in root mats within diatomites, calcilutites, and in soils developed on quartz sand in damplands of the Bassendean Dunes

Occurrence of organic matter rich material	% organic matter in root mat or in soil prior to fire	% organic matter in root mat or in soil after fire
root mat zone in diatomite filled dampland A, Melaleuca Park	90.4 + 5.6	4.4 + 0.2
root mat zone in diatomite filled dampland B, Melaleuca Park	22.2 + 4.2	2.8 + 1.3
root mat zone in diatomite filled dampland C, Melaleuca Park	81.4	3.4 + 3.3
root mat zone in calcilutite-filled sumpland 163, Becher Point area	28.1 + 24.4	5.9 + 3.6
soil on sand-floored dampland (Gnangara wetland A)	29.6	7.0 + 3.1
soil on sand-floored dampland (Gnangara wetland B)	3.4 + 0.3	1.5 + 0.6
soil on sand-floored dampland (Gnangara wetland C)	1.6 + 0.4	1.6 + 0.1
soil on sand-floored dampland (Gnangara wetland D)	2.3	1.3 + 0.6

oxidised. For the soils developed on quartz sand, while fire did not alter substrate microtopography, the organic matter content of the soils was significantly reduced in three of the four wetlands (Table 2).

The information and discussion above is not meant to imply that the response of wetland sediments and soils to fires is simple. It is complex, and dependent on a range of factors. These include: the level of the water table in the wetland at the time of the fire, the extent of the capillary rise in relation to sediment type and its effect in moistening the surface materials, the type of vegetation inhabiting the wetland influencing the calorific value of the initial fuel (e.g., fuel-rich and dense shrub and tall sedges versus fuel-poor herblands like Centella asiatica or low cover such as Baumea juncea), the recent fire history of the vegetation (e.g., extent of dry fuel development on the wetland floor, and post-fire vegetation recovery and its physiognomy which also influences the calorific value of the fuel), the dryness of the vegetation in relation to season and to water stress, the biochemical nature of the organic-matter-rich wetland substrate, and the mineral nature of the sedimentary and diagenetic particles residing with the organic mater in the substrates. Nevertheless, Figure 4B and data for wetlands A and C in Melaleuca Park in Table 2 provide empirical information on materials that are flammable, and hence provide an indication of the composition of wetland materials that are likely to combust under dry conditions. In this context, it is the peat and diatomaceous peat that are flammable sediments, and root mat zones that are flammable soils.

Pyrosediments, formed as residues after combustion of diatomaceous peat, organic matter enriched calcilutite, peaty sand, or tree trunks with termite structures (see later) commonly are texturally and compositionally similar to the lithologically equivalent primary sediment described above, viz., diatomite, calcilutite, and quartz sand. Some pyrosediments are new products of combustion, e.g., fine-grained calcite crusts, anhydrite, alkaline metal carbonates, sulphates, and chlorides, goethite, and haematite. Pyrosediments also may manifest specific colouration, surfaces, structures, or geometry developed as a result of fire, e.g., orange to red staining due to fire-induced oxidation of iron sulphides, fire-sculptured (irregular to scalloped) surfaces, heat-indurated surfaces, deep cracks (to be filled by later sediments, such as mud, or intraclast breccia), in situ breccioid structures, and millimetre-scale lensoid structures resembling flaser layering (Semeniuk & Semeniuk 2004).

The diverse sediments and soils that comprise wetland basin fills on the Swan Coastal Plain are composed of various autochthonous biogenic sedimentary (i.e., formed within the wetland basin), allochthonous sedimentary (i.e., delivered to the wetland basin from external sources), and diagenetic components. These sedimentary and diagenetic components respond to combustion in a number of ways. In the first instance, they may provide the basic fuel that drives the fires. In the second instance, they hold a reservoir of particle types (as biochemicals, plant matter, biogenic particles, and various mineral species) that upon combustion or intense heat release various elements and compounds into the environment: (1) as chemically transformed material remaining in situ; (2) as ash; and (3) as smoke and gases. These components are: organic matter, biogenic silica (diatoms, phytoliths, sponge spicules), quartz silt, metal and metalloid sulphides (e.g., pyrite, arsenopyrite), and carbonates (calcite, Mg-calcite, and aragonite).

A core from a peat wetland on the Swan Coastal Plain is shown in Figure 6, illustrating the lithologic sequence, the content of selected elements (Ca, Fe, S, Pb, As, and S),
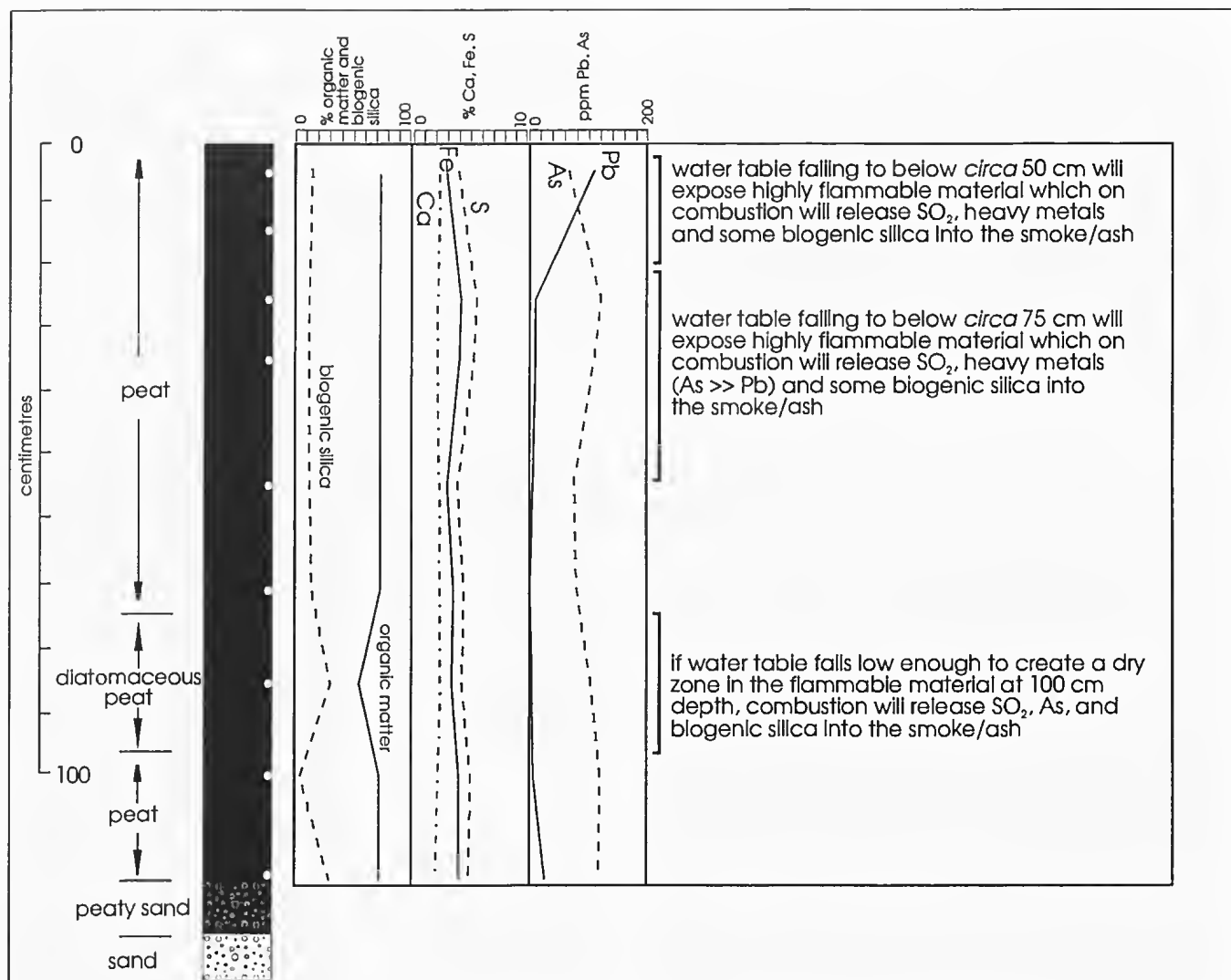
Figure 6. Annotated core from a peat wetland on the Swan Coastal Plain showing lithologic sequence, content of organic matter, % of biogenic silica, % Ca, Fe, and S, content of Pb and As in ppm, and pyrogenic implications of the geochemical and biochemical layering of the stratigraphy. The core represents continuous sampling and small circles on the stratigraphic column represent locations where samples were obtained for chemical analyses.

the percentage of organic matter and biogenic silica, and the implications of the geochemical and biochemical layering of the sediment in relation to pyrogenesis. The mineral content of peat determined by XRD is illustrated in Figure 7A & 7B, showing that in these particular peats biogenic silica, quartz, pyrite and arsenopyrite are the main mineral components – these will be the minerals that will be transformed by combustion (Table 3). In other peats, calcite and Mg-calcite may form minor additional mineral components.

Combustion of wood and sedges generates calcite ($CaCO_3$), anhydrite ($CaSO_4$), halite (NaCl), sylvite (KCl), syngenite ($K_2Ca(SO_4)_2.H_2O$), and other salts of the alkaline metals. After a fire, these minerals remain in the ash on the wetland floor, as a thin layer, or ribbons, or lenses, the latter two mirroring the local array of woody trunks, woody branches, multi-stemmed shrubs, or sedge tussocks (Fig. 8). Combustion of peat and root mats similarly generates calcite, anhydrite, halite, sylvite, and in addition, with the oxidation of metal/metalloid sulphides, depending on the temperature, goethite and haematite. Mineral components of plant- and peat-

derived ash are mobilised later by meteoric or groundwaters (*viz.*, halite, sylvite), or by wind (as dust), or remain as pyrosediment residues (*viz.*, calcite) contributing to the stratigraphic accumulation (Semeniuk & Semeniuk 2005a).

Laboratory combustion of various sediment types (*e.g.*, peat *sensu stricto*, and diatomaceous peat), and TEM and EDS analyses of smoke deriving from these materials indicate that different types of mineral species within smoke are generated from different types of sediments (Fig. 9). Specifically, Figure 9 shows that mineral components within the wetland sediment (such as biogenic silica) *are* mobilised into the smoke, that compounds generated by combustion from plant material and organic matter are also mobilised into the smoke (e.g., $CaSO_4$, NaCl, and silicates, amongst others), and that smoke can be source-specific, (*i.e.*, biogenic-silica-rich peat will generate silica-bearing smoke).

Some of the morphological, mineralogic and textural changes effected on biogenic silica by experimental combustion are shown in Figures 7C, 7D and 10. Heating diatomite or sponge spicules in a combustion oven for 1

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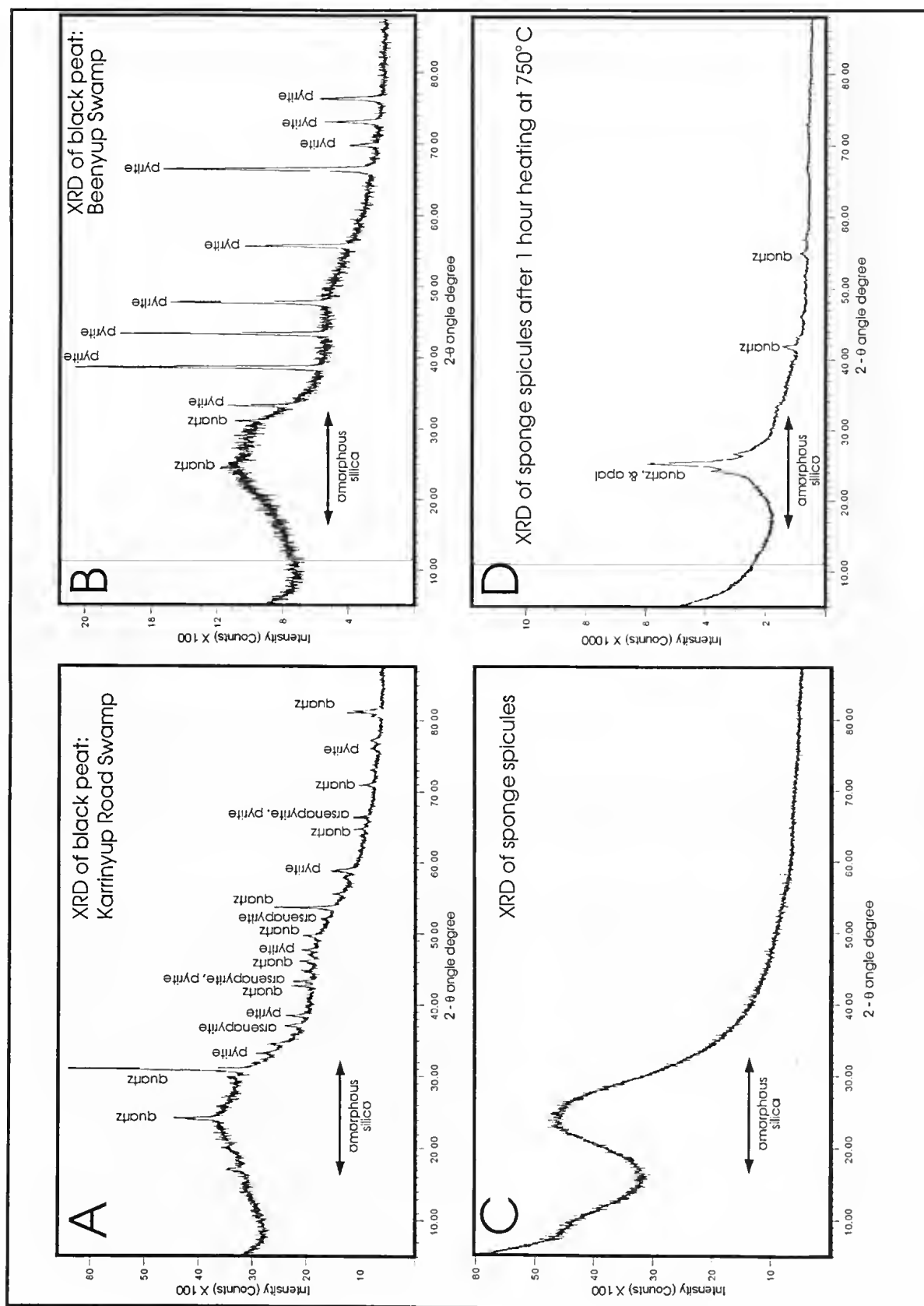
Figure 7. A–D. X-ray diffractometry of peat and sponge samples using Co Ka radiation. A & B. Occurrence of pyrite and arsenopyrites in peat. A. Black peat from Karrinyup Road Swamp showing biogenic amorphous silica, quartz silt, pyrite, and arsenopyrite. B. Black peat from Beenyup Swamp showing biogenic amorphous silica, pyrite, and minor amount of quartz silt. C & D. Crystalline silica developing from biogenic silica (note scale difference in y-axis between C & D). C. Diffractometry for spicules collected from a living sponge. D. Crystallisation of silica in the spicules from the same sponge as above after heating at 750° C for 1 hour.
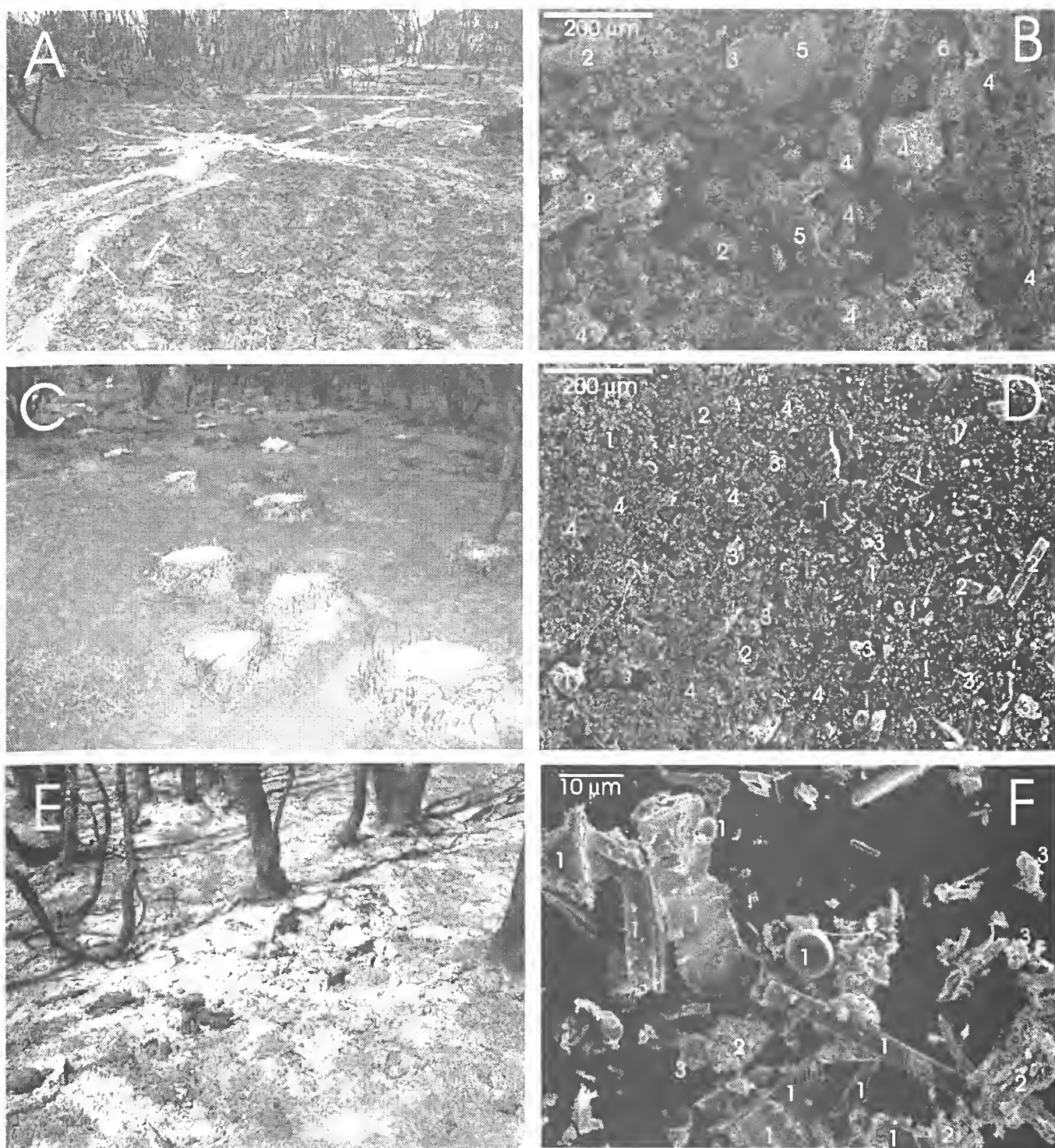
Figure 8. A–D Field and compositional aspects of ash. A. Ribbons of ash (composed of calcite, anhydrite, and other alkaline metal salts, as determined by XRD), c 2 mm thick, deriving from the combustion of wood, and mirroring the array of woody branches and trunks along the vegetated periphery of a wetland. B. SEM photomicrograph of the ash in (A) showing the fine grained material and aggregates; composition of particles determined by EDS, as annotated on the photomicrograph, are: 1. silica; 2. NaCl; 3. dominantly $CaSO_4$; 4. mixed $CaSO_4$, $CaCO_3$, NaCl and SiO_2; 5. dominantly NaCl, with $MgSO_4$ and $CaCO_3$. C. Lenses of ash (composed of phytoliths, calcite, anhydrite, and other alkaline metal salts, as determined by XRD), c 10 cm thick, left as residuals at the base of combusted tussocks of sedges. D. SEM photomicrograph of the ash in (C) showing the fine grained material and aggregates; the elongate particles are phytoliths, or phytoliths with adhering salts; composition of particles determined by EDS, as annotated on the photomicrograph, are: 1. biogenic silica (phytolith); 2: biogenic silica (phytolith), with adhering NaCl, KCl, $CaSO_4$; 3. mixed $CaSO_4$, $CaCO_3$, NaCl and SiO_2; 4. mixed NaCl, KCl, $CaSO_4$, $MgSO_4$, and $CaCO_3$. E. Crusts of diatomite collapsed around the base of burnt trees where root mats have been burnt away leaving ash. F. Annotated SEM photomicrograph of the ash in (E) showing the fine grained non-flammable residual biogenic material (diatom fragments, sponge spicules, phytoliths) and aggregates of salts derived from combusted organic matter; note spherical silica melt globule (or micro-droplet) in centre of photomicrograph field; composition of particles in the ash determined by EDS, as annotated on the photomicrograph, are: 1. biogenic silica (diatom fragments, sponge spicules, phytoliths, and spherical silica globules); 2. dominantly SiO_2 (as platelets = diatom fragments) and $CaCO_3$, with minor mixed NaCl, KCl, $CaSO_4$ and $MgSO_4$; and 3. dominantly NaCl. SEM and EDS work undertaken with assistance of Rick Hughes (CSIRO).

hour and for 2 hours at 250° C, 500° C, 750° C, and 1000° C results in the partial crystallisation of the X-ray amorphous silica to crystalline silica with increasing temperature (Fig. 7C & 7D). Petrographic microscopy shows that at higher temperatures 750–1000° C, the newly developed crystalline nature of sponge spicules becomes evident along the periphery of the spicules as birefringence (*i.e.*, optical anisotropy; Kerr 1959). This type of heating also results in the partial melting and change of morphology of the spicules, in their progressive fragmentation, and in the production of silica globules and micro-droplets (Fig. 10).

A brief description of the potential response of the various autochthonous sedimentary, allochthonous sedimentary, and diagenetic constituents of wetland sediments to combustion, based on the literature, field observations, and our laboratory combustion experiments, is presented in Table 3 below. Details of the various experimental procedures carried out in the laboratory and sampling following fires in wetlands in the field are provided in Semeniuk & Semeniuk (2005a).

Wetland stratigraphy

The term "wetland stratigraphy" refers to the sequence of sediments and soils that underlie wetlands, which on the Swan Coastal Plain are basins, channels or flats. The study of wetland stratigraphy involves investigation of sediment layering, the sequence of sediment types, the relationship of sediment fill to the base and margins of the wetlands, and the changes in sediment types (as facies) across a wetland. On the Swan Coastal Plain, the various types of sediments in wetlands described earlier may form stratal sequences composed entirely of the one sediment type, homogeneous mixtures of these sediment types, interlayered sequences of the sediments, or texture-mottled mixtures of the sediments. The mesoscale interlayering of various sediments within the wetland sequences (*i.e.*, interlayering in 50 cm or 100 cm units) is related to: 1. changes in climate through the Holocene, driving sedimentation, for example, from diatomite-dominated to peat-dominated, or calcilutite-dominated to sand-dominated; and 2. evolution of wetland hydrochemistry, driving sedimentation, for example, from calcilutite-dominated to peat-dominated (Semeniuk 2005), or diatomite-dominated to peat-dominated.

For basins, sediment fill in wetlands within the Swan Coastal Plain, as measured in the basin centre, varies in thickness from 0.1 m to 7 m (Semeniuk & Semeniuk 2005b), though most wetland sedimentary fill is 1–1.5 m thick. For peats, it ranges from 0.3 m to 7 m. For deposits of calcilutite, it ranges from 0.2 m to 5 m. For diatomites, the thickness ranges from 0.1 to 3 m. For kaolinitic mud deposits, the thickness ranges from 0.1 m to 1.5 m. The base of wetland fills tends to be gradational into the underlying Pleistocene materials, *e.g.*, peat, diatomite, or calcilutite overlying "basement" sand have a gradational zone of infiltrated or bioturbated wetland sediment resulting in development of peaty sand, diatomaceous sand and calcilutaceous sand, respectively (Fig. 11A). The margins of the wetland fills also may have an interfingering relationship with reworked deposits of the

Table 3

Response of the various autochthonous sedimentary, allochthonous sedimentary, and diagenetic constituents of wetland sediments to combustion.

Sedimentary and diagenetic particle types	Response to combustion
organic matter (fine-grained, as well as leaves, twigs, branches) and dry plant material	conversion mainly to CO_2, and various other complex hydrocarbon gases, SO_2 and NO_2; generation of smoke composed of varying carbonaceous particulate material; release of K, Na, Ca, and Mg, and their transformation into alkaline metal carbonates, sulphates, and chlorides, which may be mobilised into the smoke or may remain residual as ash; release of nutrients from the plant detritus
biogenic silica (*i.e.*, diatoms, phytoliths and sponge spicules, as micromorphologically diagnostic, X-ray amorphous silica)	when temperatures are high enough, fine-grained particles may be converted (in part) to crystalline silica, or may partially melt, developing deformed shapes, beaded tips, and melt micro-droplets; sponge spicules and diatoms fracture and fragment into finer particles; both fine-grained biogenic silica and any fire-generated crystalline silica, as well as melt micro-droplets may be mobilised into the smoke plume, and that which remains as ash may later be mobilised by wind
quartz silt	inert to combustion, but able to be mobilised into the smoke plume
metal and metalloid sulphides	oxidation of metal and metalloid sulphides to oxides (*e.g.*, pyrite to goethite and haematite), and SO_2, and their mobilisation into the smoke plume, or remaining as residua in the ash; the metal/metalloid oxide residues remaining in the wetland deposits later may be mobilised by wind or by meteoric and ground waters
calcite, Mg-calcite, aragonite	combustion temperatures usually not high enough to progress the wholesale transformation of $CaCO_3$ to CaO, but fine-grained carbonate grains can be mobilised into the smoke
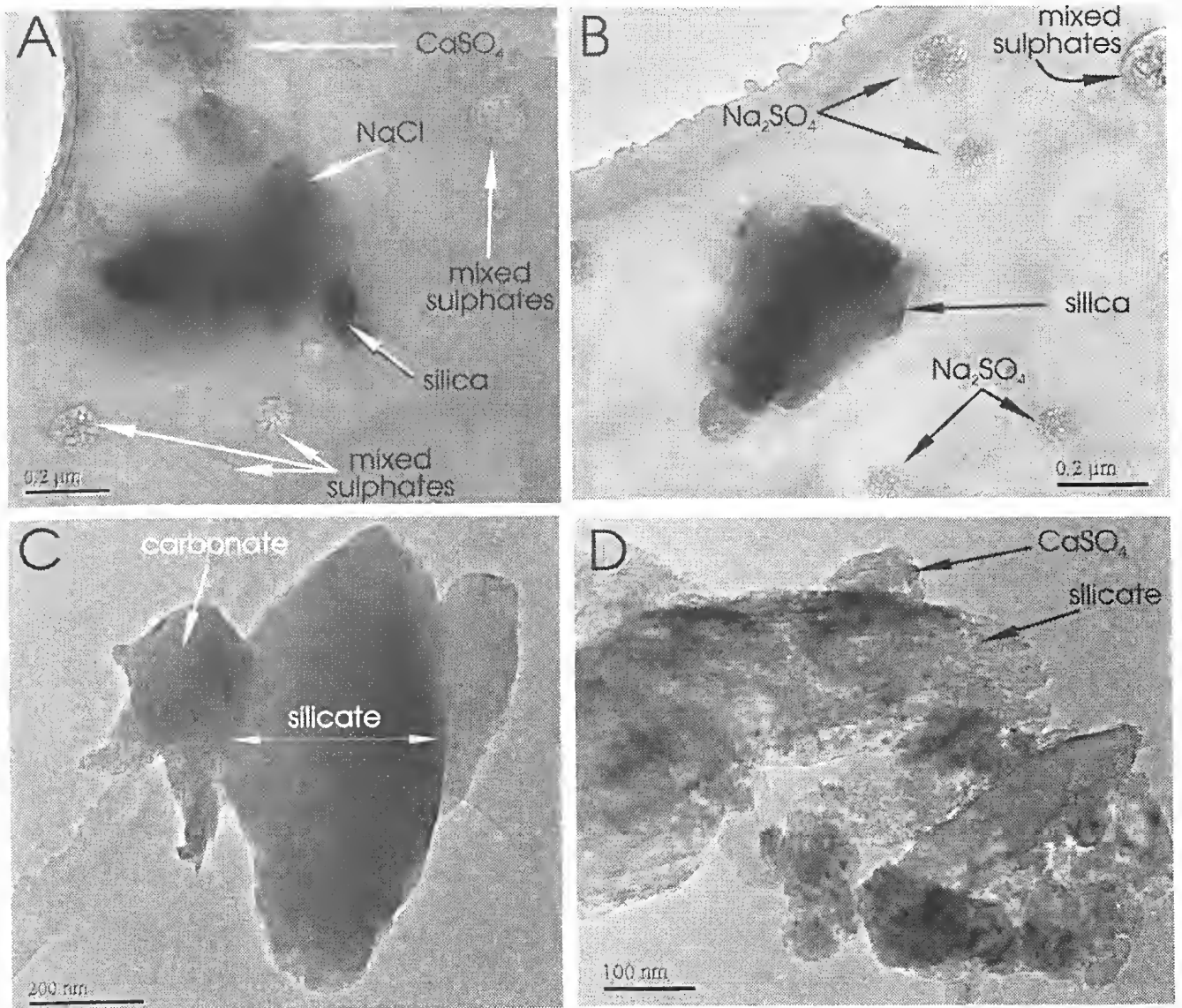
Figure 9. Images from transmission electronic microscopy (TEM) of smoke from a diatomaceous peat and from a peat, both experimentally combusted at 550° C. Collection grid was held above the burning material in the smoke of each for 20 sec to collect the samples. Images were taken by T A Semeniuk at ETH Zurich using bright field modes with a Phillips CM30 operated at 200 kv. Bright field images were supplemented by EDS to determine elemental composition. Mineral and particle phases are annotated to illustrate differences in smoke composition. A & B are from diatomaceous peat. C & D are from peat *sensu stricto*.

surrounding Pleistocene sediments (Fig. 11B). Thus, peat, diatomite, or calcilutite of central wetland basins may grade *via* peaty sand, diatomaceous sand, and calcilutaceous sand into the quartz sand of the Pleistocene margins, or sheets and tongues of quartz sand reworked from the margins may penetrate to a limited distance into the layers of the wetland fills.

Other factors contributing to wetland fill and variation in wetland stratigraphy include coastal aeolian influx (either as grainfall deposits *via* suspension in the air, or as grainflow deposits from migrating dunes), and fire, where interlayered peat and other sediment types are reduced to peat-free layers. In addition, through the process of groundwater fluctuations, wetland-fill and host materials in wetlands may be overprinted by bleaching and by development of ferricrete (Semeniuk & Semeniuk 2004).

Thirteen standard sequences are recognised in the sedimentary fill of wetlands by Semeniuk & Semeniuk (2005b) in the central Swan Coastal Plain in Bassendean Dunes and Spearwood Dunes and Pinjarra Plain; and two additional sequences are recognised in the Quindalup Dunes by Semeniuk (2005), giving a total of fifteen standard sequences. These standard sequences, with some variation in thickness of units therein, recur throughout the wetlands of the Swan Coastal Plain. The standard sequences and type locations (where best developed) are listed in Table 4.

In addition, there are wetlands, particularly damplands set in the Bassendean Dunes, that do not have sedimentary fill, but rather have humic soils or organic matter enriched soils developed on a seasonally-waterlogged "basement" of Bassendean Sand.
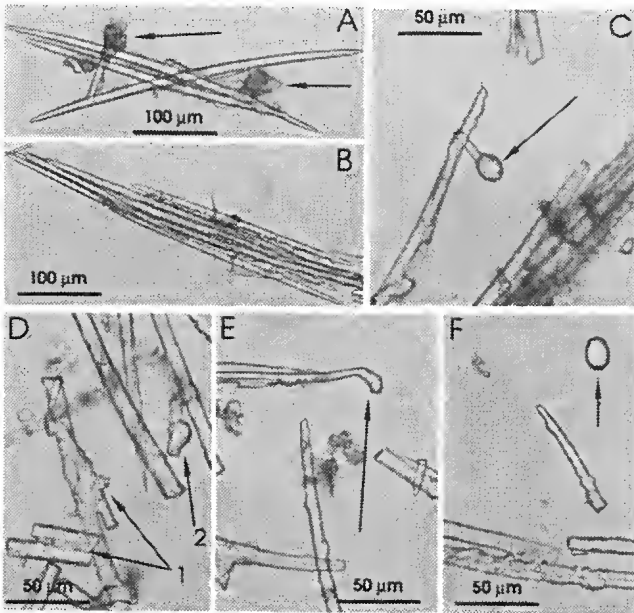
Figure 10 A–F. Photomicrographs of sponge spicules. A & B. Spicules from a living sponge showing smooth to slightly spiny external form of the spicules, the unfragmented (entire) nature of the spicules, and their distinct sharp tips; material connecting the spicules (arrowed) is dried sponge organic matter. C–F. Changes in the morphology of spicules after heating for 1 hour at 750° C. C. Normally sharp tip of spicule transformed by partial melting to form a globule (arrowed). D. Several spicules have fused through partial melting (arrow 1), a tip has melted to form a globule (arrowed 2), and there is a predominance of spicule fragments. E. Normally sharp tip of spicule distorted through partial melting (arrow). F. Spicules are predominantly fragmented, and a solidified micro-droplet of silica (arrow) is now isolated from the spicules.

Geographic distribution of stratigraphic types in wetlands

Knowledge of the distribution of the various types of wetland sediments and soils is a powerful tool in fire management because it allows for focus on critical areas where there is high potential for flammable sediments and soils to occur. On the Swan Coastal Plain, there is a pattern to the distribution of wetland sediments and soils and stratigraphic types geographically from east to west and from south to north. The east to west distribution is related to consanguineous suites (as related to geomorphic setting), and the south-north distribution is related to climate.

The stratigraphy of the wetland fills varies according to geomorphic and geologic setting, climate, and host water chemistry. The various consanguineous wetland suites, for example, reside in different geomorphic and geologic settings each with its own basement materials of white quartz sand, yellow quartz sand, limestone, quartzo-calcareous sand, and fluvial terrigenous sediments. In each setting, groundwater and surface water maintenance of the wetlands may vary, and hydrochemistry also will be affected by water source and geologic setting (e.g., quartz sand, limestone, or quartzo-calcareous sand). Hence there occurs a variety of sedimentary fills in any east-west transect.

Channels and wetland flats (rivers, creeks, floodplains, and palusplains) associated with terrigenous sediments of river courses that occur on the Pinjarra Plain, or the Pinjarra Plain transition to Bassendean Dunes, along the eastern Swan Coastal Plain, tend to be underlain by extrabasinal sediments, such as sand and kaolinite-dominated mud and muddy sand, reflecting their delivery and sedimentation by fluvial processes, and basins within the Pinjarra Plain, or the Pinjarra Plain transition to Bassendean Dunes (e.g., within the Mungala, Bennett Brook and Keysbrook Suites) are filled with peat, terrigenous muds or muddy sand.

Within the Bassendean Dunes, where the basin setting is a basement of quartz sand, the wetlands are lakes, sumplands, and damplands. The waters tend to be tannin-rich, acidic (to alkaline), and cation-poor, and the sedimentary fill is intrabasinal peat, diatomaceous peat, and diatomite (reflecting their hydrochemical setting), and extrabasinal kaolinitic mud, and quartz sand. These sediments may form sequences composed entirely of the one sediment type, or homogeneous mixtures, interlayered sequences, or texture-mottled mixtures of the sediments. Wetlands in the various consanguineous wetland suites in the Bassendean Dunes, depending on climate setting, may be peat-dominated (e.g., Jandakot Suite and Riverdale Suite in southern Swan Coastal Plain areas), or peat-and-diatomite dominated (e.g., Gnangara Suite and Jandakot Suite in central Swan Coastal Plain areas), or diatomite-dominated (e.g., Jandakot Suite in northern Swan Coastal Plain areas).

Within Spearwood Dunes, where the basin setting is a basement of quartz sand and/or limestone, the wetlands are lakes and sumplands. The waters are more variable, ranging from tannin-rich to tannin-poor, alkaline (to acidic), and cation-enriched, and the sediment fills are intrabasinal peat, diatomaceous peat, or calcilutite, and extrabasinal quartz sand. Again, the sedimentary fills also may form sequences composed entirely of the one sediment type, or homogeneous mixtures, interlayered sequences, or texture-mottled mixtures of the sediments. Wetlands in the various consanguineous wetland suites within the Spearwood Dunes may be peat-dominated or with mixed peat-and-calcilutite (e.g., Yanchep Suite), or peat-and-calcilutite dominated (e.g., Stakehill Suite), or calcilutite-dominated (e.g., Coogee Suite). The types of sedimentary fill in the basins reflect their hydrochemical setting in relation to local occurrence of quartz sand or limestone and their geomorphic setting in relation to reworking of quartz sand.

Within the Quindalup Dunes, where the basin setting is a basement of quartzo-calcareous sand, the wetlands are lakes, sumplands, and dampland. The groundwaters are of variable hydrochemistry, ranging from tannin-rich to tannin-poor, alkaline (to acidic), and cation-enriched, and the sedimentary fill is intrabasinal calcilutite (reflecting the hydrochemical setting), and some peat, and extrabasinal quartzo-calcareous sand. Wetlands in the various consanguineous wetland suites within the Quindalup Dunes are calcilutite-dominated (e.g., Becher Suite and Cooloongup Suite), or humic sand and calcilutaceous muddy sand dominated (e.g., Peelhurst Suite).

A summary of the east-west pattern of sedimentary
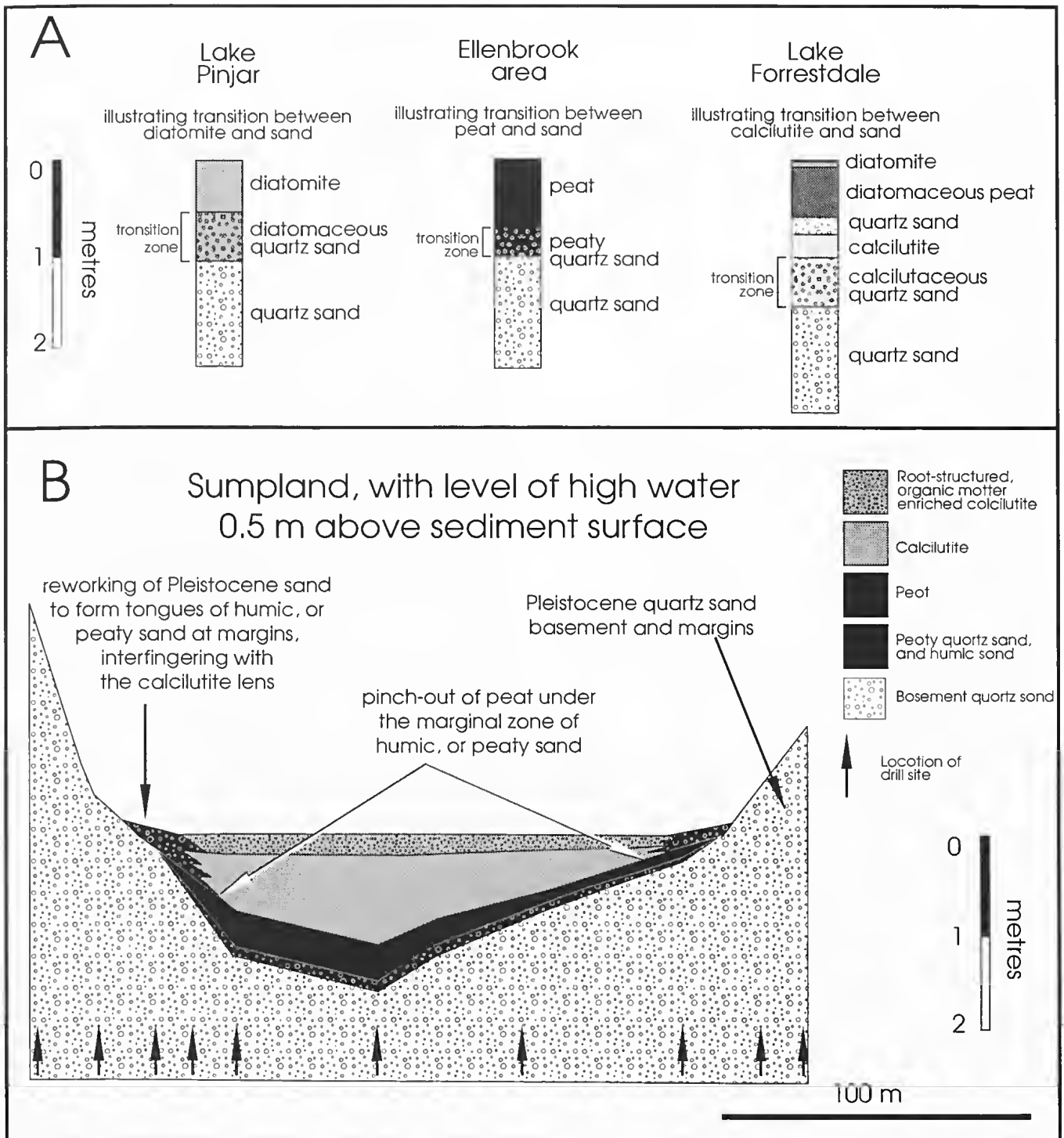
Figure 11. A. Examples from three sites showing typical transitions of fine-grained wetland sediment (diatomite, peat, and calcilutite) into underlying basement sand with the development of "muddy" sand. B. Stratigraphic profile of a sumpland (Little Carine Swamp). The basin is mainly filled by calcilutite, but with tongues of humic or peaty sand extending into the wetland from the margins. The peat at depth pinches out under the margins of the wetland, and a humic soil is developed on the calcilutite deposit.

fills in wetlands related to geomorphic settings on the Swan Coastal Plain is shown in Figure 12.

The Swan Coastal Plain, extending from Busselton to Dongara, traverses a climate from subhumid (annual rainfall c 1000 mm) to semi-arid (annual rainfall c 500 mm), with a concomitant increase in evaporation. In response to this climate gradient, from south to north, similar wetland basins change in their vegetation cover,

hydrologic dynamics, hydrochemistry, and sedimentary fills. Wetlands within Bassendean Dunes provide an excellent example of climate-controlled patterns in sedimentary fill.

Throughout their longitudinal extent, the Bassendean Dunes exhibit a regionally similar template of basins and hills, inherited as desert dune landforms from the Pleistocene. The basins commonly intersect the regional

Table 4

Standard stratigraphic sequences within Swan Coastal Plain wetlands

Style of stratigraphy	Typical location[1]
Dominantly peat sequences	
thick peat	Karrinyup Road Swamp
thick peat and diatomaceous peat	Waluburnup Swamp
thin peat and diatomaceous peat	Melaleuca Park Swamp
Dominantly diatomite sequences	
thick diatomite	North Lake
thin diatomite and diatomaceous sand	Lake Pinjar
Dominantly calcilutite sequences	
thick calcilutite	Lake Manning
thin calcilutite	Cud Swamp
thin peat on thin calcilutite	Wawa Swamp
Terrigenous sequences	
kaolinitic mud	Lake Mungala
Mixed sequences	
peat, calcilutaceous peat, and diatomaceous peat	Stakehill Swamp
diatomite, calcilutite, and quartz sand	Lake Forrestdale
alternating peat and calcilutite	Leda Swamp
peat, calcilutite, quartz sand	Little Carine Swamp
peat, kaolinitic mud, quartz sand	Ellenbrook Swamp
diatomite, kaolinitic mud, quartz sand	Coonabidgee Swamp

[1] Stratigraphic types are described in Semeniuk & Semeniuk (2005b)

water table, resulting in a series of wetlands (Semeniuk 1988), and depending on the extent and depth that basins intersect the groundwater, the wetlands may be permanently inundated, seasonally inundated, or seasonally waterlogged. To the south, the basins have accumulated peat under sedges; they support mixed paperbark trees and sedges that cover the wetland. To the north, they have mostly accumulated diatomite, and support heath and paperbark trees, often confined to the basin margins. The transition from southern to northern types is gradational because of the mixed contribution of regional and local influences. It is largely the climatic setting that underpins the different vegetation associations and the different sedimentary fills across the latitudinal spread of these wetlands.

The same pattern exists for wetlands within Quindalup Dunes and Spearwood Dunes, *i.e.*, peat dominating southern areas, and calcilutite and diatomite in the north.

Water levels, water tables and climate

Management of fire-susceptible substrates is linked not only to their distribution, but also to the periods when such substrates are most susceptible to ignition and combustion. Clearly, substrates that are permanently inundated, or permanently waterlogged are not likely to ignite and combust, but an annual fluctuation of a water level or water table, however, can result in an annual drying out of potentially combustible substrates (Fig. 13). Figure 14 illustrates a range of annotated hydrographs from various wetlands on the Swan Coastal Plain

showing the types of water level changes over the past decade, and their implications for substrate flammability. Further, if water levels or water tables exhibit progressively increasing annual fluctuations, or a progressive fall in mean low water level, the latter linked to a trend towards drier periods in medium and long-term climate patterns, then management of organic rich substrates will also have to address these changes.

Water levels and depth of water table are linked to annual rainfall, and variability in rainfall is related to climate variation. Notwithstanding that there is a current emphasis on correlating climate variation in southwestern Australia with the effects of mean sea level pressure and surface sea temperatures (Allan & Haylock 1993; Nicholls *et al* 1999; Smith *et al* 2000; Sadler 2002), tentatively linked by some authors to the phenomenon of El Nino – Southern Oscillation (also known as ENSO), we give emphasis to the fact that many of the natural climatic patterns of the Earth ultimately are underpinned by astronomical phenomena. The most obvious and well known is the annual progression of seasons driven by the orbit of the Earth and the tilt of the Earth's axis to the orbital plane. In the Perth region, this is expressed as the cool/cold, wet winters and the hot, dry summers. There are, of course, a range of other astronomical processes, orbits, and alignments that result in climatic expression on the Earth, and an understanding of these patterns helps to explain some climate dynamics (Fairbridge 1984), with the caveat that any astronomical effect on Earth climate may be accompanied by a time lag, so that direct correlation becomes blurred, particularly for the shorter term (decadal, or bi-decadal) cycles. Astronomical phenomena affect Earth climate through variable solar radiation, through tidal forcing of the atmosphere, by changing the heat capacity of the oceans through tidal perturbations, amongst other processes.

The main astronomical patterns that appear to be cyclic or periodic, and their relationship to the various climatic patterns, and in particular rainfall, are described in Table 5.

In regards to the effect on climate of the Lunar Nodal periodicity, there may be consensus that there is a *c* 20-year cycle in climate in relation to rainfall and drought (Currie & Fairbridge 1985; Tyson 1986; Semeniuk 1995a), which has been correlated with the 18.6-year Lunar Nodal periodicity, but some authors suggest that this climate pattern could also be related rather to the 19.9-year Saturn-Jupiter cycle, or to the 22-year double sunspot (or "Hale") cycle (*cf.* Camuffo 1999). Though proximal effects, such as Lunar tidal effects, probably have stronger influence on Earth climate than distal phenomena, we accept this caution.

While underpinned by solar radiation, the El Nino – Southern Oscillation phenomenon, with a return period of some 3–4 years, varying to 6–8 years, is not strictly periodic but is a quasi-periodic intra-planetary phenomenon.

Important features of cycles and periodicities in climate are that, firstly, they are predictable, secondly, they may affect the flammability of wetland sediments, and thirdly they may imprint on wetland sediments such that their products then provide a record that can be used to reconstruct past climates, and predict future climate
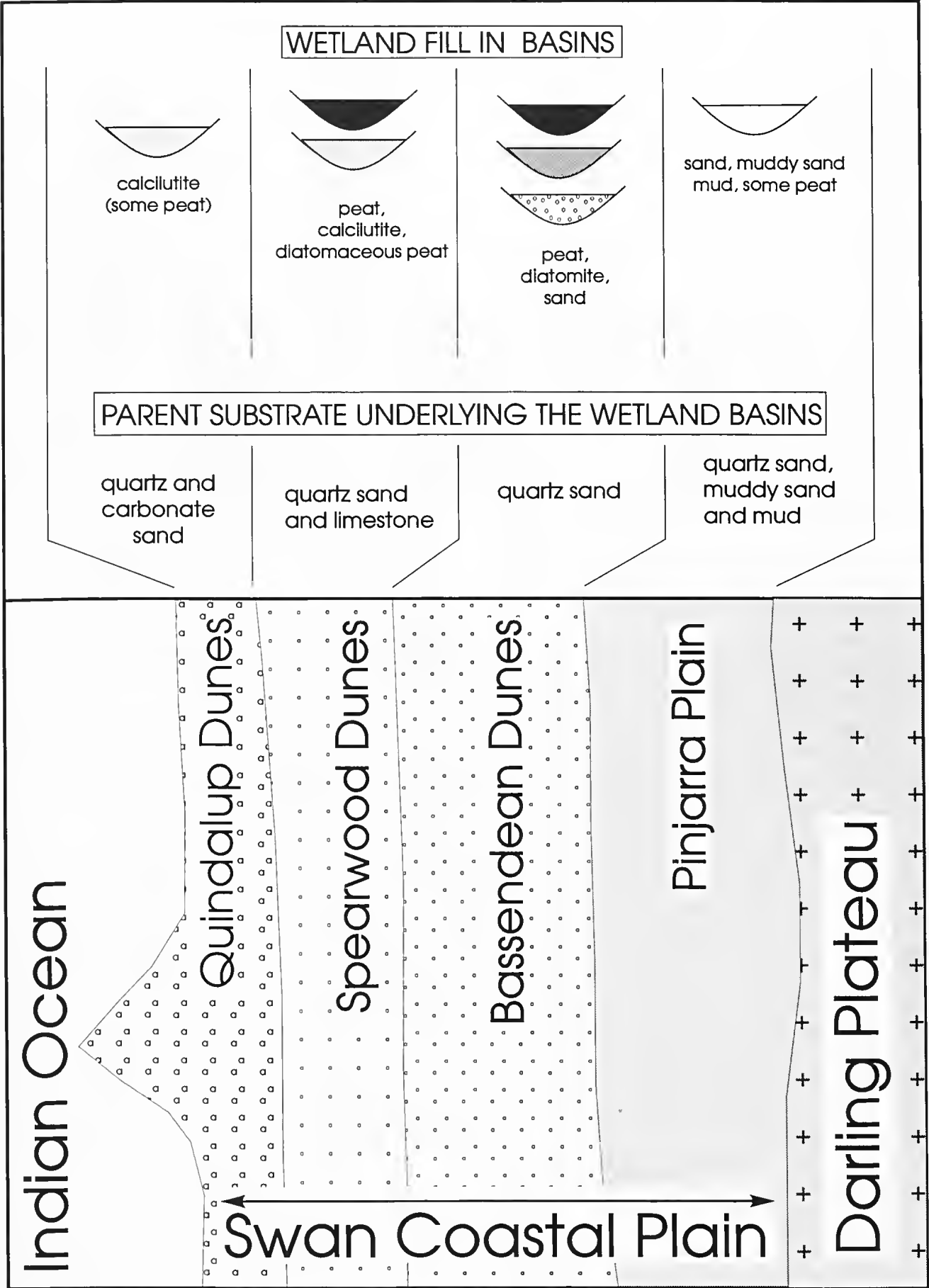
Figure 12. Idealised diagram summarising, with respect to geomorphic setting across the Swan Coastal Plain, the distribution of parent substrate types underlying wetland basins and the (simplified) wetland sediment types in basins.

trends. In these contexts, climate patterns are particularly important as tools in fire management.

While there may also be some influence from a human-induced greenhouse effect, we consider that the effects of the Lunar Nodal Periodicity (the c 20-year cycle), the 250-year cycle, and the Earth-axis precession on rainfall, water levels, and fluctuating water tables to be of particular interest for the management of wetlands, water levels, and the temporal occurrence of fire-susceptible substrates in that these phenomena carry with them some degree of predictability. Perth has a long-term rainfall record of c 120 years, and the patterns of c 20 year wet-and-dry intervals related to the Lunar Nodal Periodicity appear to be evident here (Semeniuk 2005) when the annual rainfall data are processed using a 10-year backward moving average (Fig.13). The effects of the 250-year cycle also may be partially evident in this record, if the relatively high rainfall period between 1920–1960 corresponds to the peak of rainfall within this cycle. Processing annual rainfall data using cumulative deviations from the mean rainfall (Yesertener 2005) shows a broadly similar pattern for the Perth rainfall record: a period of increased rainfall in the years 1920s–1970s is amplified using this procedure (cf. figure 2 of Yesertener 2005), and smaller amplitudes corresponding to increased and decreased rainfall on a c 20 year pattern are also evident. The effects of the Earth-axis precession on climate are not evident in the historic rainfall record but are partially evident in the Holocene stratigraphic record (Semeniuk 1995a) as a long-term trend towards a wetter climate.

From the perspective of the flammability of wetland sediments and soils, management of fire in wetlands should address the potential that there may be a short-term recurring pattern of drying out and wetting of wetland sediments on a c 20-year cycle, and a similar drying out and wetting on a longer term 250-year cycle because it is during those times of relatively dry climate phases that the greatest risk of combustion occurs. The c 20-year cycle of wet and dry years is a fairly regular event, and can readily explain the phases of wet years and dry years in the wetlands of the region. However, the question arises that if there is a 250-year cycle in rainfall in the southwest Australian region, where in this cycle does the current climate reside? If it is concluded that the period of maximum rainfall and elevated water levels that occurred during the 1920s–1970s coincided with the maximum rainfall within the 250-year cycle, then the trend thereafter has been towards the minimum dry phase, and it can be expected that there will be another 40–50 years of progressively drier periods, with shorter-term, superimposed lower amplitude 20-year cycles of wetter and drier phases. A summary of the patterns, and its implication to fire management is presented in Figure 13.

Anthropogenic use of water causing draw-down, drainage, waste water disposal, or silviculture such as pine plantations, can artificially affect water levels, and replicate, rival or exceed the effects of climate variability on water levels and water tables (Fig. 13). Thus, drying of wetland sediments, leading to increased risk of combustion, can be the result of water abstraction, draining, or silviculture, and is an issue that also must be addressed in fire management.

Observations and stratigraphic information on the effects of fire in wetlands

Mapping and monitoring wetlands for 30 years (Semeniuk & Semeniuk, 2005c) have provided opportunities to observe and document the effects of fire in wetlands in a number of locations on the Swan Coastal Plain in removing peat, altering lithology (i.e., creating pyrosediments), creating distinctive stratigraphy, or fundamentally altering the wetland type and its vegetation associations. The information below presented from a range of wetlands exemplifies these effects. The wetlands selected are: Melaleuca Park (31° 40' 21" E, 115° 54' 15" S), Waluburnup Swamp (31° 47' 08" E, 115° 48' 14" S and 31° 47' 28" E, 115° 48' 25" S) and Beenyup Swamp (31° 47' 16" E, 115° 48' 00" S) of Yellagonga Regional Park, Bullrush Lake (31° 29' 29" E, 115° 39' 17" S), Yarkin Swamp (31° 47' 38" E, 115° 59' 43" S), and Ellenbrook (31° 45' 14" E, 115° 58' 18" S).

In the summer of 1976 in the Melaleuca Park area and during the 1980s in Beenyup Swamp, a series of fires swept through the peat-floored wetland basins. Some 20 cm of peat was removed by the combustions, similar to that described in peatlands by Horwitz et al (1999) in southern Western Australia, and the roots of Melaleuca rhaphiophylla trees within the wetlands were left standing above the sediment surface. The base of the burn-out in each case was the zone of capillary rise of the water table. This type of surface, developed by fire, often is irregular to hummocky, and is stained by oxidized iron. Such surfaces are recognisable in the stratigraphic record, and have been noted as buried surfaces in Little Carine Swamp and Lake Gwelup.

In 1985, while documenting wetland stratigraphy at Bullrush Lake, the effects of a fire that had been recently burning were observed. While there was a thin cooled crust on the surface, augering showed that there was still a furnace of burning peaty sediment for at least 30 cm in depth. During this fire, spongolitic diatomaceous peat was reduced to spongolitic diatomite (in this case, a pyrosediment) with the removal of organic matter. The iron sulphide of the peat was oxidized to iron oxide (haematite and goethite), imparting a red to orange coloration to the pyrosediment at the surface.

In May 1996, a fire swept through part of Waluburnup Swamp. While this fire consumed the vegetation, the monitoring bores emplaced by the V & C Semeniuk Research Group showed that the water table at the time was rising at the beginning of winter, and was only 10 cm below the sediment surface. The sediments were too waterlogged for combustion. Elsewhere, in this same wetland, where the water table was lower due to more rapid groundwater discharge, the fire consumed and removed the upper 5 cm of the peat profile; below this level, the peat was too waterlogged for combustion.

In 1992, fire swept through the margin of Yarkin Swamp, a peaty sumpland. The margin of this wetland was peaty sand overlying quartz sand at c 30 cm, and with vegetation cover of the Flooded Gum, Eucalyptus rudis. Termites constructed sand-structured termitaria within the trunks of the Flooded Gum, deriving the sand grains from under and within the peaty sand. Fire reduced the Flooded Gums to ashes, and the sand-structured termitaria, interior to the tree trunks, were

A Annotated graph of 10-yr backward moving average annual rainfall for Perth region using *circa* 120 years of records

During the wet phase of the 1920s to 1950s, the end-of-summer water levels were above the peat surface; the peat was water-saturated and not flammable

During 1991, the wet phase of the 20-year cycle, the end-of-summer water levels were at or just below the peat surface; peat remained water-saturated, or moist, with low flammability

During 1996, the dry phase of the 20-year cycle, the end-of-summer water levels were well below peat surface: the peat was desiccated and became flammable, with higher probability for combustion if ignited

C Responses of a peat-filled basin to climate-induced variation of rainfall shown in Inset A and water levels shown in Inset B

trending towards drier years

wetter years

22 yrs

20 yrs

21 yrs

20 yrs

19 yrs

mean annual rainfall ~120 yrs of records

1991-2000: 10 years of decreasing rainfall reflected in falling water levels in the hydrograph shown in B.

Rainfall in mm

B Annotated hydrograph of monthly water level in a wetland between 1991-2001, showing lowest water levels reached during a relatively wet period *versus* a relatively dry period

surface of sediment is at 3.5 m AHD

low water level at 3.3 m AHD in May 1991

0.7 m difference in low water levels between May 1991 and May 1996

low water level at 2.6 m AHD in May 1996

declining water levels in response to declining rainfall

AHD (m)

Figure 13. The relationship of climate variation (expressed in rainfall), water levels in wetlands, and potential flammability of fire-susceptible wetland sediments. A. Annotated graph showing medium term wet and dry phases, ranging from c 19–22 years, evident in the rainfall records of Perth over the past 120 years using the 10-year backward moving average (note that since the averaging procedure involves the previous 10 years of data, the wet and dry periods will be displaced along the time axis). B. Hydrograph showing details of 10 years of water level response to declining rainfall during the wet-to-dry transition within a "20-year" cycle, and the position of the wetland floor and water levels. C. Predicted response in regard to fire susceptibility of a peat-filled basin to the wet-and-dry climate phases depicted in inset A and B.

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Table 5

Summary of astronomical cycles/periodicities and climate patterns (discussed for Western Australia by Glassford 1980 and Semeniuk 1995a)

Cycle/periodicity/pattern[1]	History and/or description	Climate effect
Milankovitch cycles (also known as the Croll-Milankovitch cycles[2])	formulated by Croll (1867a,b) and Milankovitch (1941) to explain the recurring glacial and interglacial periods, and other climatic changes, driven by variation of the Earth's orbit and rotation in terms of its eccentricity, tilt of rotational axis, and longitude of perihelion, with periods of return on a c 100,000 year, 41,000 year, and 23,000 year pattern; in this analysis, precession forms a component of astronomic events that drive glacial/interglacial periods	drives glacial/interglacial cycles, and hence the associated major arid to relatively humid climate changes over tens of millennia
Earth-axis precession	rotational precession of the Earth's axis, with a return period of c 19,000–23,000 years	drives the progressive migration of the calorific equator, and hence the gradual latitudinal shift in climate during the Holocene; for instance, will drive the long-term general increase in humidity in southwestern Australia over millennia
250-year pattern[3]	a high-frequency cycle of c 250-year period, empirically determined by Stocker & Mysak (1992) and Semeniuk (1995a) that at present appears to have no astronomical underpinning, though the temporally similar 245-year periodicity of Loutre et al (1992) has been related to Earth orbit parameters	evident in the larger beachridges at Rockingham that form every c 250 years (reflecting oceanic storminess and wind patterns), and for wetlands; will drive long-term wet and dry cycles in rainfall
Double-Hale cycle	solar phenomenon, where the sunspot activity varies on a 45-year cycle (Fairbridge & Hillaire-Marcel 1977)	evident in the smaller beachridges at Rockingham that form c every 50 years; not clearly reflected in rainfall variation
Solar sunspot 11-year cycle	solar phenomenon, where a pattern of increasing and decreasing sunspot varies on an 11-year pattern	generally, no clearly documented effect on climate, but Currie & Fairbridge (1985) link this phenomenon to cyclic 11-year induced droughts and floods
Lunar Nodal periodicity	the Lunar node rotates once every 18.6 years in the nodal cycle, and once every nine years the lunar node is oriented toward the Sun, causing syzygy to coincide with zero declination of the Moon; in this paper, the Lunar Nodal periodicity is informally termed the c 20-year pattern	reflected in relatively wetter and drier phases in rainfall on a c 20-year rainfall pattern (Currie & Fairbridge 1985), e.g., in South Africa, North America, China, and southwestern Australia[4]

[1] terms and definitions for astronomical, celestial mechanics and geodesy are provided in Munk & Macdonald (1960), Vanicek & Kratiwsky (1982), and Matzner (2001);

[2] while commonly known in the literature as the Milankovitch Cycles, there has been a tendency in recent years to term this effect as the Croll-Milankovitch cycles, or Croll-Milankovitch Theory, in recognition of the important and early part that Croll played in the development of glacial theory and astronomic forcing (cf. Muller & MacDonald 1997)

[3] there appears to be a c 250-year climate pattern reflected in ice cores (Stocker & Mysak 1992), and in the repetitive construction of large beachridges on the Rockingham-Becher Plain (Semeniuk 1995a); Bradley (1999) reports the work of Loutre et al (1992) who calculated (from changes in precession, obliquity and eccentricity) various significant high-frequency periodicities, one of which was 245-year, and considers these high-frequency periodicities to be important in climate variability on the decadal to century timescale; while these calculations are for the northern hemisphere, and while Berger et al (1993) have shown there can be an asymmetry in climatic response across the latitudes and from northern hemisphere to southern hemisphere, the generalised insolation pattern for the northern hemisphere can be applied to the southern hemisphere;

[4] Borisenkov et al (1983), in calculating variation in terrestrial insolation resulting from perturbations in Earth's orbital parameters, report on a 18.6-year periodicity, which they ascribe to nutation of the pole, induced by lunar gravitational attraction and the inclination of the Moon's orbital plane to the plane of the ecliptic; c 20-year rainfall patterns are reported in South Africa by Tyson (1986) and Currie (1993), North America by Currie (1984) and Currie & Fairbridge (1986), China by Currie & Fairbridge (1985), and southwestern Australia by Semeniuk (1995a).

reduced to small conical piles of sand, which in time with rain wash became thin lenses of sand (a pyrosediment). Thus, fire can transform the stratigraphy of homogeneous peaty sand to one of peaty sand with scattered small, discrete thin lenses of sand.

In 1986, during a study of wetlands in the Ellenbrook region by V & C Semeniuk Research Group (Semeniuk & Semeniuk 2005c), a wetland basin was classified and described as a sumpland, underlain by 20 cm of a sequence of peaty sediments (peat, sandy peat and peaty sand), and vegetated by *Baumea articulata*. In the next ten years, following a general falling of the water table regionally, there was a drying out of the shallow sedimentary sequence. A fire swept through the wetland in the summer of 1993, and burned out the peaty sediments, exposing the underlying sand (noted in Figure 13B). After the fire, during the period 1993–2004, the wetland had become a sand-floored dampland, vegetated by *Melaleuca preissiana* and *Astartea fascicularis*. Thus, fire had removed the peaty substrates,
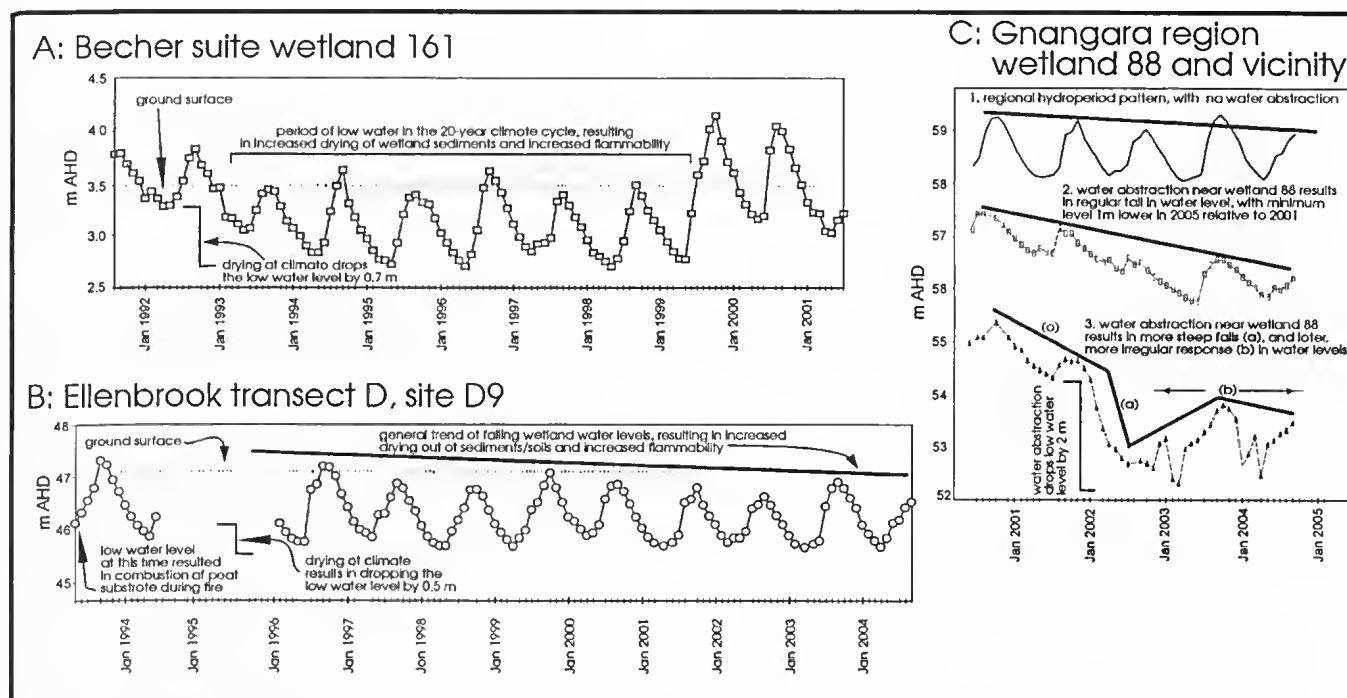
Figure 14. Annotated hydrographs from three wetlands on the Swan Coastal Plain from Semeniuk (2005) and Semeniuk & Semeniuk (2005c) showing: (1) hydroperiods and the natural and anthropogenically-induced trends in falling water tables (dark line), (2) location of ground-surface (stippled line) relative to the water level, and (3) the potential for flammability of the wetland sediment/soil. A. Becher Suite wetland 161 (Semeniuk 2005) exhibits falling, then rising water levels, and a period of increased flammability. B. Ellenbrook transect D shows falling wetland water levels in response to a drying climate, and the period when peat substrates combusted along this transect. C. Gnangara region wetland 88, and vicinity, showing wetland water level responses to water abstraction; hydroperiod (1) shows the hydroperiod pattern in the region, where there is no water abstraction, i.e., a low decline in water levels; hydroperiod (2), a moderately steep decline in water levels as a result of water abstraction; hydroperiod (3) shows steep decline and irregular fluctuations in water level as a result of water abstraction; in this region, peat substrates in wetlands that exhibit hydroperiods (2) and (3) have increased potential for combustion. Note that the vertical scale in (A) is 2 x that of (B) and (C).

and in concert with a generally falling regional water table, the wetland was transformed from a peat-floored sumpland to a sand-floored dampland, with attendant changes in vegetation.

Discussion and conclusions

In Western Australia, to date, minimal use has been made of information on wetland sediments or wetland hydrologic patterns in formulating strategies and policies for fire management (Fire & Rescue Services of Western Australia 2000; SEMAC 2002; Auditor General W.A. 2004). Yet, as a result of accidental, poorly timed, or too frequent fire regimes, there have been varying pyrogenic effects on wetlands and their sedimentary fill, (depending of course on their lithological characteristics), varying responses in the combustion of wetland materials (e.g., different types of fires, and different types of secondary effects deriving from these fires), and varying effects on the surrounding environment from the burning of wetlands.

Information on wetland sediments, wetland stratigraphy, and hydrologic patterns is important in the management of fire for many reasons:

1. the type of wetland sediment (e.g., the composition of the peat) combined with the degree of moisture content, in relation to the depth of the water table

at a given time of year, can determine the calorific value of the sediment and the intensity of the ensuing fire;

2. annual and longer term hydrologic patterns determine when wetland sediments become susceptible to burning;

3. in a stratigraphic context, regionally falling water tables over the long-term result in fires coming in contact with progressively deeper stratigraphic layers (with different sediment types, or different geochemistry), and consequently different combustion regimes and geochemical responses;

4. the heavy metal and metalloid content of the sediment, the type of parent plant material that originally formed the peat, the alkaline metal content of the decomposing plant material, the sulphide content of the peat, and the diatom, phytolith, and sponge spicule content of the burning substrate can result in various types of smoke, with implications for community health;

5. the oxidation and chemical perturbation of the wetland sediments during a fire and the development of a labile chemically complex ash result in a substantially different geochemical environment in the wetland, with implication that the post-fire situation can have a subtly altered wetland hydrochemistry;

6. the development of ash noted in (3) introduces various types of mineral species into the wetland, and this may be mobilised as dust by post-fire aeolian processes, with implications for community health;

7. burning of wetland sediments results in the destruction of wetland stratigraphic geoheritage.

These reasons clearly point to the necessity of accruing information on wetland sediments and having a framework for predicting the occurrence of the different types of wetland sediments and their stratigraphy. This information would then be coupled with historical data on water table levels in wetlands to be used for fire management purposes. Basic information on wetland sediments, water tables, and the stage of flammability of wetland sediments and soils, in connection with both the annual and longer term climatic patterns, would lead to the identification of wetlands at high risk to combustion, and the identification of high risk periods that may result from short or long-term low water tables and reduced saturation.

We suggest that fire management in wetlands requires design and implementation of pre-emptive strategies (*i.e.*, before fires are ignited) and operational strategies (to be undertaken during fire events), pertaining to sedimentological, stratigraphic, mineralogic, geochemical, and hydrologic properties of a wetland. The principles and information presented in this paper can assist with both. For instance, information on the distribution of wetland sediments in regard to landscape setting, climate, wetland type, and the temporal variation of material flammability, responding to fluctuating or declining water tables, provides a powerful tool in pre-emptive fire management. Knowledge of the stratigraphy of a wetland is an important tool in pre-emptive and operational fire management in that firstly stratigraphy provides information on the reservoir of flammable material available for combustion, and secondly, the stratigraphic array of flammable material along the wetland margins provides insight of how fire can access the surface and subsurface flammable material.

Drawing on information on sediment types and stratigraphy of wetlands from Semeniuk & Semeniuk (2004, 2005b), this paper provides a basic description of the variety of wetland sediments on the Swan Coastal Plain, broadly relating their occurrence and distribution to landscape setting east to west across the Coastal Plain, to the south to north climate gradient, and to hydrology. There is a strong relationship between composition of the wetland sedimentary fill, and landscape setting and wetland type, as well as between the sedimentary fill and geographic/climate setting, and this relationship provides a basis to broadly predict the occurrence and distribution of potentially flammable material in wetlands across the Swan Coastal Plain.

In a wetland, the basic materials that are susceptible to combustion pass through stages of high to low combustion potential, depending on the annual cycle of the falling and rising water table, and on the longer term climatic cycles. Hydrological data from wetlands at risk, incorporating annual water table fluctuations, and longer term regional trends, can be used to extrapolate material flammability.

From a chemical perspective, wetlands, comprising wetland vegetation and peat, are a reservoir of various mineralogic, geochemical and biochemical species that, after transformation during burning, can be mobilised into the atmosphere during the fire, by wind after the fire, and into the groundwater after the first rains following the fire. Setting aside the issue of wetland vegetation which is a source of fuel to a fire above the substrates of a wetland, stratigraphic sequences, surface sediment types, and soils underlying wetlands comprise the basic combustible material of fires in the substrates of wetlands, and data on these materials should thus form the first stage information base in the design of any pre-emptive fire management and operative fire management in wetlands, because their variability in terms of content of organic carbon, type of plant material contributing to the organic carbon, biogenic silica, quartz silt, alkaline metals, heavy metals and metalloids, and sulphide content can influence the type of fire and type of smoke generated, and influence post-fire environmental processes.

While wetland sediments have been described by Semeniuk & Semeniuk (2004) in terms of textures (*i.e.*, grain size fractions), mineralogic composition, the nature of their gravel, sand and mud-sized constituents, and the occurrence of fine-grained framboidal pyrite as microcrystalline FeS_2, the details of the heavy metal and metalloid content of wetland sediments, their stratigraphic occurrence, their mineralised geochemical setting, their hydrochemical setting, and the full implication of this variability in pyrodynamics are beyond the scope of this paper. However, in this paper attention is drawn to the fact that during an intense burn of wetland sediments and soils, in addition to the combustion and transformation of the organic matter in the wetland sediments, the other fine-grained constituents, either remaining as residues after combustion (*e.g.*, quartz silt), or geochemically or crystallographically transformed by the combustion (*e.g.*, sulphides, and biogenic silica), can be mobilised into the atmosphere with the smoke. Smoke is generally known to be a complex mixture of carbon, tars, liquids, particulate matter, and various gases that include carbon monoxide, aldehydes, nitrogen oxides, peroxides, acids, and products deriving from chlorine-bearing and nitrogen-bearing polymers (Ward & Hardy 1991; Andreae *et al* 1996), and studies elsewhere have highlighted the variability of emissions from biomass burning in terms of the biochemical and metal/metalloid species present in smoke, and their effects on human health (Allen & Miguel 1995; Yamasoe *et al* 2000; Andreae & Merlet 2001; Johnston *et al* 2002; Page *et al* 2002; Graetz & Skjemstad 2003; Lemieux 2004). However, while there has been an emphasis in the literature on the chemical composition of smoke, there has been less information on its mineralogy.

The matter of crystallographic transformation of biogenic silica during a fire and the mobilisation of this silica into the smoke is an important one in that crystalline silica (cristobalite) is a known carcinogen. Normally crystalline silica occurs as equant grains, but biogenic silica transformed partially to crystalline silica, albeit in low concentrations, retains its spicular or fibre form, and as such is toxic. Fubini (1998) considers

biogenic silica converted to crystalline form to be one of the most fibrogenic forms of silica. Ash, left as a residual after a fire, also can be mobilised into the atmosphere later by wind. The material comprising these smoke and ash assemblages would include: the fine-grained particles of quartz silt and primary biogenic silica; biogenic silica transformed partly or wholly into crystalline silica by the heat during combustion; solidified micro-droplets of melted silica; the oxidised sulphides of heavy metals and metalloids (and other derivatives such as SO_2); and the carbonates, sulphates and chlorides of the alkaline metals. The issue is important to address because smoke and aeolian-mobilised ash deriving from burning and burnt wetlands may locally affect nearby communities, or affect specific susceptible members of the community. The potential health problems associated with generally inhaling smoke from biomass burning are discussed in Johnston *et al* (2002), Aditama (2000), Jalaludin (2000), and those associated with inhaling biogenic silica, and biogenic silica partially crystallised to cristobalite are discussed by Rabovsky (1995), Merget *et al* (2002), Stratta *et al* (2001), and Fubini (1998).

In summary, in relation to smoke and dust, chemically, with its cocktail of pyrogenic compounds, smoke is known to affect community health, but the matter of the pyrogenic mineral species in the smoke (and post-fire dust), and their effect on respiratory health has not been adequately addressed in the literature, and in many instances, not even recognised as a potential health issue. Knowledge of the range of sediment types in wetlands, as described in this paper, provides the first step in dealing with this matter, by indicating the wetland substrates that potentially pose, through combustion, some risk to community health. Stratigraphy and geomorphic setting are highlighted herein as the bases for predicting the nature of the *mineralogic and geochemical reservoir* that may contribute undesirable constituents to the smoke during the fire, to the atmosphere by aeolian mobilisation of ash, or later, through groundwater and meteoric water interactions with pyrogenic residues, to the groundwater.

The sediments that underlie wetlands can range from those with very low or nil susceptibility to combustion (*viz.*, diatomite, calcilutite, quartz sand, and kaolinite-dominated mud and muddy sand) to those that are highly or moderately susceptible to combustion (*viz.*, peat, diatomaceous peat, and spongolitic peat), with the flammability of the latter suite depending on the location of the water table, the vertical extent of the zone of capillary rise (the zone of wetting above the water table), the extent of drying out of the material underlying the wetlands, and the percentage of potentially combustible material. It should be noted, though, that all wetland basin sedimentary fills that have high content of organic matter in their soil (the upper 10 cm), or in their sediment profiles, or have dense root mats in the shallow subsurface, have some degree of flammability, or at least, potential for rapid oxidation in hot fires. Also, given the potential for variability of sediment types across a wetland, and the interlayering of buried organic-rich sediments along the wetland margins, the stratigraphy of wetlands needs to be addressed to determine the extent of flammable materials within a wetland. It particularly needs to be part of operational management where

surface fires have already obviously occurred, and appear extinguished, but continue to burn, or smoulder in the subsurface. In this context, stratigraphy of wetlands should form a part of the information base needed to pre-emptively manage fire in wetlands, or to design on-site responses to a fire already underway.

At an ecosystem level, hydrogeological level, and hydrochemical level, the consequences of fire on water quality and aquatic ecosystems have been investigated by a number of authors: Johnson & Needham (1966), Humphreys & Craig (1981), Richter *et al* (1982), Helvey *et al* (1985), Belillas & Roda (1993) and Townsend & Douglas (2000) to determine what effects, if any, emanate from the burnt landscape, and reviewed for organic rich substrates in wetlands by Horwitz & Sommer (2005, this issue). Studies to date, however, have focused on dryland forests and heaths and the changes to soil nutrients and effects on waterway chemistry following a fire. The contributions to hydrochemical perturbations on waterways as a result of fires are manifold, including that induced by introducing ash into the environment, that resulting from increased soil erosion from the burned landscape, and that induced by changes in vegetation uptake. The effects of fires on hydrochemistry *within* wetlands, however, remain largely unexplored. Axiomatically, in wetland systems where vegetation, soils, nutrient storage and recycling, hydrology, and hydrochemistry are intimately linked (Semeniuk 2005), fires will have major effects, all with consequences for wetland hydrochemistry: reducing the store of elements within the vegetation and the substrate to ash, involving soluble labile and insoluble components; transforming minerals in the soil to their oxidised phases; removing elements and nutrients *via* smoke; and affecting aspects of wetland hydroperiod.

It is suggested that fire management strategies for wetlands be extended to the transitional zones around wetlands. In prescribed burning, it is probably advisable not to burn wetland buffer zones, or zones transitional between wetland and upland, where they are narrow, as they may not constitute a major fire risk, but where it is considered that wide buffer zones need to have a reduction in surface fuel, caution should be exercised with the timing of such an event, ensuring that wetland sediments are adequately saturated and therefore least combustible.

Thus, in summary, it is suggested that pre-emptive and operational management of fire in wetland sediments and soils should be based on knowledge of a number of factors: 1. their organic carbon content; 2. their mineralogic, geochemical and biochemical content; 3. the hydrology of a wetland; 4. the potential of wetland sediments to combust in relation to fluctuations of the water table in response to the seasons; 5. the potential of wetland sediments to combust in relation to longer term climatic patterns; 6. the areal extent of flammable material across a wetland; 7. the nature of any stratigraphic interlayering along the wetland margins; 8. the (predictive) distribution of sediment types in wetlands across the Swan Coastal Plain; and 9. the distribution of sediment types in wetlands along the climatic gradient of the length of the Swan Coastal Plain.

Whereas much emphasis in fire management to date has been placed on either the prevention or extinguishing

of fires in wetlands because of the health, industrial, and property risks they pose, the importance of protecting wetland sediments and sedimentary records *per se* from fire has been largely overlooked. However, the Western Australian State Government objectives to conserve heritage features and promote sustainable ecology, as well as the mounting scientific evidence pertaining to the archival sedimentary records (Backhouse 1993; Pickett & Newsome 1993), require these aspects of wetland sedimentary fill to be addressed in fire management as part of geoheritage (Semeniuk & Semeniuk 2000). Fire can destroy the sedimentary record of wetlands (involving for example, pollen, diatoms, isotopic and other constituents, and fossil higher plant material) that provide geohistorical and biotic information of the evolution of the wetlands in terms of palaeoclimatology, palaeohydrochemistry, and palaeo-ecology (as discussed in Semeniuk & Semeniuk 2004). The protection of wetland sediments themselves also is integral to protecting wetland habitat and preserving the biodiversity resulting from the interplay between wetland sediment geochemistry and hydrogeology, *i.e.*, between wetland sediments/soils and water (*cf* Semeniuk 2005). Thus it is suggested that the preservation of both the information contained in complete, undisturbed stratigraphic sequences within wetlands and the sedimentary environment itself should be important goals in fire management, and organisations/groups responsible for fire management should endeavour to embrace them.

Recognition that wetland sedimentary fill is a mineralogic, geochemical and biochemical reservoir that potentially can produce hazardous smoke and dust during and after a fire should not be the basis of managing wetlands as a toxic management issue. Wetlands provide invaluable information in their stratigraphic sequences (Weiss *et al* 2002), and as discussed above, are sites of geoheritage and biodiversity significance. From the perspective of geoheritage and biodiversity, the complexity of wetland substrates should be the basis for their protection for inter-generational equity. In addition, the stratigraphic, mineralogic, geochemical and hydrochemical array in the wetland profile is interrelated, and as mentioned above, is the *foundation* of wetland biodiversity. We stress, therefore, that fire management should be focused on fire prevention, on education, and in sound town planning, and not on modifying and managing the wetlands.

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Water quality responses to fire, with particular reference to organic-rich wetlands and the Swan Coastal Plain: a review

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Abstract

The unconfined aquifers on the Swan Coastal Plain provide the population of Perth with much of its scheme water and the questionable effects of fire on the quality of surface and ground water, and recharge volumes, remain unanswered. In addition, recent concerns about fire in organic sediments and the effects of groundwater decline on acid sulphate soils have increased the need for research. Based mainly on a review of relevant literature, we formulate hypotheses as to the possible effects of fire on water quality in wetlands, particularly organic-rich ones, on the Swan Coastal Plain. Water quality responses may occur due to catchment effects (increased runoff and erosion, explainable by removal of canopy cover and changes in soil water repellency, resulting in nutrient and sediment fluxes into the wetland, elevated cation concentration and a shift to alkalinity) and atmospheric effects (the return to the ground of dissolved volatilized reactive and particulate compounds). For both these effects, on the Swan Coastal Plain the over-riding catchment influences are the ways in which the wetlands interact with the shallow unconfined aquifers and how a fire and a changed fire regime might affect this relationship. Profound changes to water quality are possible upon rehydration of burnt or overheated (organic) soils. Cracking and erosion caused by fire can expose acid sulphate soils to oxidizing conditions, resulting in lower pH and mobilization of heavy metals. Superimposed on all these changes are the trophic consequences and how they might influence water quality. Finally we discuss the secondary effects that arise from management attempts to control or prevent fire in a wetland, such as fire suppression effects, flooding or trenching to stop a peat burn, or prescription burning around a wetland to reduce fuel loadings, each of which might trigger or exacerbate any of the above mentioned water quality responses. Management should therefore apply a precautionary approach to prevent irreversible losses (like erosion of organic soil profiles) and otherwise use an adaptive management approach to test the hypotheses stated herein.

Keywords: fire, water quality, organic-rich wetlands, Swan Coastal Plain, acidification

Introduction

Assessments of the impact of fire rarely examine consequences for water quality, and by extension aquatic biodiversity. This is probably because wetlands are perceived to be beyond the influence of fire. On the Swan Coastal Plain in Western Australia there are several reasons why this shortfall of knowledge needs to be addressed. The unconfined aquifers on the Plains provide the population of Perth with much of its domestic, industrial and commercial water and the questionable effects of fire on the quality of surface and ground water, and recharge volumes remain unanswered. In addition, fire in organic sediments is a growing concern (Horwitz *et al.* 1999; Horwitz *et al.* 2003), as are the effects of groundwater decline on acid sulphate soils (Sommer & Horwitz 2001; Appleyard *et al.* 2004).

The Swan Coastal Plain (SCP) can be characterized as a bioregionally heterogeneous wetland system composed of permanent and ephemeral shallow lakes in depressions as well as sumplands, damplands and palusplains, dissected by occasional creeks and rivers discharging into estuarine lagoons (Semeniuk 1987). On the plains wetlands are related to the ridges and interdunal depressions of the three dune systems that run north-south, and parallel with the coastline, over the western two-thirds of the Swan Coastal Plain (Seddon 1972). The unconsolidated Quaternary deposits on the SCP form a regionally extensive unconfined aquifer known as the 'superficial aquifer'. There are two major groundwater flow systems in the Perth region known as the Gnangara Mound and Jandakot Mound (flow systems) (Davidson 1995). Although some of the wetlands are perched, the majority interact with the groundwater table in some way.

Water quality in the wetlands is a reflection of the particular geomorphic unit on which they are situated. Thus wetlands on the Quindalup and Spearwood Dunes tend to be well buffered, with neutral to relatively high pH (a reflection of the underlying calcareous and limestone sediments), while wetlands on the strongly leached Bassendean dunes are generally coloured, poorly buffered and acidic (Water Authority of Western Australia 1995). By extension, the water quality response to any disturbance, including fire, will also be strongly dictated by their geomorphic settings. Another important factor influencing water quality response is the amount of organic matter in the aquatic sediments. The wetlands

under discussion have varying amounts of organic matter, ranging from very low levels to true peat sediments with the proportion of organic matter content, in some cases, in excess of 80 % (Teakle & Southern 1937).

Most of the wetlands are surrounded by at least a minimal buffer of either bushland (with those in better condition often as declared State nature reserves), or parkland gardens managed by local government authorities. By virtue of their urban or semi-rural settings, the wetlands are invariably, and regularly exposed to accidentally or maliciously lit fires. Often the fires are restricted to surrounding bushland or littoral vegetation as their progress deeper into the wetland is impeded by the presence of water.

In recent years, however, over-extraction of groundwater, exacerbated by declining rainfall, has lowered groundwater tables (in some instances markedly), and consequently wetland water levels (Water & Rivers Commission 2001). Some wetland systems, for example those on the northern and eastern Gnangara Mound (the Lexia suite of wetlands, Bombing Range wetlands, wetlands of the Yeal Nature Reserve, linear chain of wetlands between Yanchep and Lake Goolellal, and those in the Mariginiup -Gnangara suite) have in the recent past become so dry in summer that nearby fires have passed through the wetland areas, either severely cracking the organic soils or actually burning them (Fig. 1). The passage of fire into a wetland may be enhanced by the presence of introduced plants, particularly grasses (Davis & Froend 1999) and sedges.

Whether wetland organic profiles are cracked or burnt, or whether only wetland vegetation, or only the surrounding catchment is burnt, water quality will be at least temporarily affected. But how, and how will water quality changes affect the ecological values of such wetlands? The aim of this paper is to examine the literature and describe the water quality responses to fires that occur in or around wetlands, and to formulate hypotheses that state their relevance for wetlands on the SCP and other similar ecosystems.

Methods

Literature searches were conducted via knowledge bases, principally the Australian Agriculture and Natural Resources Online (AANRO)(incorporating databases of Streamline, ARRIP and ABOA) at Land and Water Australia; the Cooperative Research Centre for Hydrology's Bushfire Hydrology website; Google and Google Scholar (www.google.com and www.scholar.google.com) and the AGRICOLA database at the Water Quality Information Centre at the National Agricultural Library, Agricultural Research Service, United States Department of Agriculture. Searches were performed using the following primary keywords: fire, water quality, organic soil (or peat), in combination with the following secondary keywords: soil repellency, hydrology, nutrients, trophic response, heavy metals, acidification, review, and relevant biogeographic localities (like the Swan Coastal Plain, The Everglades, Sumatra etc.).

Figure 1. Impact of a wildfire which took place in the Bombing Range wetlands in 1995–1996. The organic sediments are cracked and exposed, showing bleached diatomaceous earth. Elsewhere sedge-pedestals and meter-deep cracked profiles were visible (not shown on photo).Cracks shown here are up to 5cm wide. Photograph B. Sommer 1997.

Although the general fire literature is extensive, comparatively little has been published on the effects of fires on water quality *per se*, and most material that does exist deals with either catchment effects (flowing water systems, for instance Townsend & Douglas 2000), in hilly or mountainous forested areas (see for example Chessman 1986; Bayley *et al.* 1992; Earl & Blinn 2000; Shakesby *et al.* 2003), or the fate of nutrients associated with burns in productive forests (see Ranalli 2004). Drawing on the identified literature sources, the general fire literature, the discussion of fire and water quality in Horwitz *et al.* (2003) and on our own experiences on the SCP, this paper discusses the potential consequences of fire on water quality in terms of:

a) catchment effects;

b) atmospheric effects;

c) rehydration of burnt or overheated (organic) soils;

d) trophic consequences; and

e) fire suppression and fire prevention effects.

In discussing these five themes, we have highlighted, where appropriate, their relevance to wetlands on the SCP.

Potential changes to water quality following a fire

Catchment effects

The potential impact of fire on wetland water quality will depend on the fire regime (the extent, frequency, intensity, season and duration of the fire), the size of the catchment affected by fire, the slope/topography of the terrain, climatic conditions, the type of vegetation, as well as moisture content and depth of any organic-rich soil (see Humphreys & Craig 1981; Ranalli 2004; Rhodes & Davis 1995). The larger and steeper the catchment, the more vulnerable the water body will be to the surrounding terrestrial environment (Rhodes & Davis 1995). The dissolvable and erodible residue of a fire will generally find its way into a wetland, changing water quality. Vegetation ash derived from the surrounding catchment is typically alkaline and rich in extractable Mg, Ca and K (Gimeno Garcia *et al.* 2000). Because of this, the pH of receiving water bodies tends to increase following a catchment fire (Ranalli 2004). Palaeolimnological records from northern hemisphere lakes show that diatom-inferred pH rises abruptly at sedimentary horizons containing evidence of fire (i.e. charcoal) (Korhola *et al.* 1996; Rhodes & Davis 1995).

It is also well known that, depending on the intensity, fire releases varying types and quantities of soil nutrients (Belillas & Rodà 1993; Christensen 1994; DeBano *et al.* 1998; McNabb & Cromack 1990). Some of these, in particular phosphorus, will be washed, blown, or diffused into wetlands from ash. For nitrogen Ranalli (2004 p.20) concluded from his review of the literature that:

> ...the major source of ammonium to surface water during and immediately following a fire is from the dissolution of ammonium volatilized from the combustion of organic matter into precipitation or

into a stream or lake. The major source of nitrate immediately following a fire is the nitrification of ammonium released from the combustion of organic matter.

Catchment hydrology effects are well described in the literature: increased water yield following fire is the norm. This results from the destruction of vegetation and litter cover, and reduced infiltration resulting from the development of water-repellency of catchment soils (Debano 2000; Emmerich & Cox 1994; Letey 2001; Rambal 1994; Scott & van Wyk 1992; Shakesby *et al.* 2003). Debano (2000) summarizes the process leading to repellency, where heat is produced by combustion of the litter layer on the soil surface, vaporizing organic hydrophobic substances, which are then moved downward in the soil along the steep temperature gradients until they reach the cooler underlying soil layers, where they condense, coating and chemically bonding to mineral soil particles. These are general effects, and exceptions do occur; Shakesby *et al.* (2003) describe a fire of sufficient heat to patchily destroy pre-fire surface repellency, rather than generate post-fire repellency. Nevertheless, the volume of water entering a wetland may be temporarily increased following a fire.

The increased water yields and surface flows over exposed soils result in increased catchment erosion (Belillas & Rodà 1993; Emmerich & Cox 1994; Menaut *et al.*1992; Wilson 1999). This in turn leads to increased turbidity in receiving water bodies. Townsend & Douglas (2000) demonstrate that the degree of erosion and amount of suspended sediment is a function of the intensity and season of the fire. Reducing the intensity of the fires allows catchment vegetation to recover, decreasing the erosive effects of raindrops and overland flow (Townsend *et al.* 2004).

On the SCP, runoff-related effects resulting from fire in a catchment might be relatively minimal and highly localized due to the low relief in the bioregion, and the small nature of surface catchments in non-urbanized parts of the Plain. Local erosional events may occur, particularly for sandy soils that are non-wetting (and hence seasonally water repellent) and exposed to infrequent heavy rainfall events in summer, depositing coarse sediment and some dissolved ions into littoral habitats of wetlands. The nature of the sediment suggests that such events are unlikely to cause significant changes in turbidity. Similarly, the alkaline ash produced from a fire in the catchment is unlikely to be washed into surface waters except from riparian areas and under the extreme rainfall circumstances described above. For groundwater dependent wetlands on the SCP the more crucial catchment-related fire issue is whether fire exacerbates the naturally water repellent sandy sediments, delaying seasonal changes to infiltration rates, and ultimately reducing groundwater recharge, and what the effect of fire intensity will be on this relationship.

Atmospheric considerations

Biomass burning releases large quantities of reactive compounds to the atmosphere, in particular NOx, hydrocarbons, CO_2 and sulphur compounds (Anderson 1996; Fishman *et al.* 1993). Large quantities of soot and organic carbon are also emitted. From here they can fall to the ground in the form of dust, or become hydrated

and return to the ground in a dissolved form with precipitation. When they fall into poorly buffered waterbodies, nitrogen and sulphur compounds dissolved in 'acid rain' may oxidize and cause acidification (Roser 1997).

Fire in organic soils is extremely difficult to extinguish. Smoke generated from peat soils is chemically different from most other types of smoke and more smoke per hectare is created than that of vegetation fires on other soil types (see Hinwood & Rodriguez 2005, this issue). Partial (restricted) combustion releases to the atmosphere a variety of chemical compounds, which not only have the potential to affect wetland water quality, but are also deleterious to human health (Fishman *et al.* 1993).

It is doubtful whether these issues are significant influences on wetland water quality on the SCP because the most probable time of the year when this rehydration would result in acidic precipitation is that season (winter) when catchment or wetland fires are least likely to occur, and when smoke would be carried eastwards by the strong prevailing westerlies. However, the water quality implications for smoke generated from wood heaters in winter, or smoke haze over the SCP from autumn prescribed burns in the lower south-west of the State requires investigation.

Rehydration of burnt or overheated (organic) soils

One of the most obvious disadvantages of fire is that it has the capacity to consume considerable amounts of accumulated organic matter. The edges of organic-rich wetlands are most vulnerable because the water level is less of an influence, the organic soils are shallow and dry out more easily and their loss exposes mineral soils more readily. The loss of organic matter from wetlands can have a number of contrasting consequences for water quality. Since much of the acidity of peat bogs is due to organic acids (Wetzel 2001), combustion of organic soils should result in an increase in alkalinity, and this in combination with the ash effects described above, should result in a rise of pH in these systems.

It would be incorrect to believe that fire invariably increases the pH of water bodies. Peat can contain large amounts of organic sulphur, not all of which is volatilized in a fire. The portion of sulphur not removed by fire could eventually become available for oxidation and the production of sulphuric acid. The peat sediments also, more often than not, contain reduced inorganic sulphur (e.g. metal sulphides such as pyrite [FeS_2]), rendering them 'Acid Sulphate Soils'. Peat on the SCP can contain up to 15 % by weight of oxidizable sulphur (Appleyard *et al.* 2004). Acid Sulphate Soils are abundant in coastal regions around Australia, including the SCP (National Working Party on Acid Sulphate Soils 2000). They largely originate from sulphate in seawater which inundated land as sealevels rose some 10,000 years ago, subsequently mixing with land sediments containing iron oxides and organic matter (National Working Party on Acid Sulphate Soils 2000). They are relatively stable under anaerobic conditions, but when exposed to air the sulphides oxidize. When subsequently wetted they react with water to produce sulphuric acid. The capacity for organic rich wetlands in south-western Australia to undergo an acidic response upon aeration through drainage has long been recognised (see Teakle &

Southern 1937), and more recently through drought and groundwater decline (Sommer & Horwitz 2001).

Complex relationships may exist between drying due to drought or other causes, and resulting acidification, and the loss of organic profiles due to subsequent fires and further water quality consequences, as evidenced by a lake in south-coastal Western Australia described by Horwitz *et al.* (1999). They found the lake water to be clear and acidic (pH 3.2 – 3.7) with extremely high redox values (360– 460 mV) before the October 1994 fire. When visited after the fire in July 1996 they noted that the dry surface of the lake was dominated by iron precipitate. They suggested that their observations imply at least two acidification events, one before and one after the fire. Drying prior to 1994 would have produced the cracks in the soil causing the oxidation of soil deeper in the profile, while the fire may have subsequently exposed passive acid sulphate layers. It was noted in Horwitz *et al.* (2003) that the inputs of alkaline ash from the burnt catchment were apparently insufficient to neutralize the sulphuric acid that formed after reinundation of the lake.

Several organic-rich wetlands on the eastern Gnangara Mound (Lexia wetlands, Melaleuca Park EPP wetland) have revealed pH values lower than 4 during routine monitoring visits (see for instance Clark & Horwitz 2004). It is not unreasonable to speculate that such low pH values could be exacerbated by fire (either burning the soil, or overheating it to produce cracks), given the relatively frequent occurrence of fire in the area. These wetlands occur on the poorly buffered Bassendean sands. Where such acidification events are possible, it can also be hypothesized that cracked soils upon rehydration will allow acidified water to enter the groundwater system, forming an acidic plume. Elsewhere on the SCP where sediments are buffered, the immediacy of the acidic response resulting from drought or fire may be delayed, or the buffering gradually eroded, as appears to be the case at Lake Mariginiup where the spring pH of surface waters has very gradually been decreasing each year over the last 4 years (Clark & Horwitz 2004) and a fire in the lake actually burnt sediment in 2002 (Fig. 2).

There are anecdotal records of horticulturalists on the SCP burning wetlands to produce an immediate alkaline response to temporarily over-ride the acidity of the soils and result in a pulse in vegetative productivity (S. Appleyard, pers. comm.), but at the same time gradually exposing more and more of the anaerobic sediments to oxidation. Such regular burning is said to be the cause of a fire at Coogee Springs in 2002 where massive soil loss occurred due to soils being unseasonally dry from local drawdown of the water table (Horwitz unpubl. data). The wetland has not refilled since and no measurements have been made of groundwater quality underneath the wetland.

Whether the pH of surface waters increases or decreases as a consequence of fire has important repercussions for other chemical characteristics of the water. If acidification occurs, minerals in soils dissolve and liberate soluble and colloidal aluminium and iron (Fitzpatrick 2003) and other metals and metalloids; under these conditions the iron and aluminum can coagulate with particulate matter and settle out, leaving the water column clear. Likewise, in extreme acidification events,
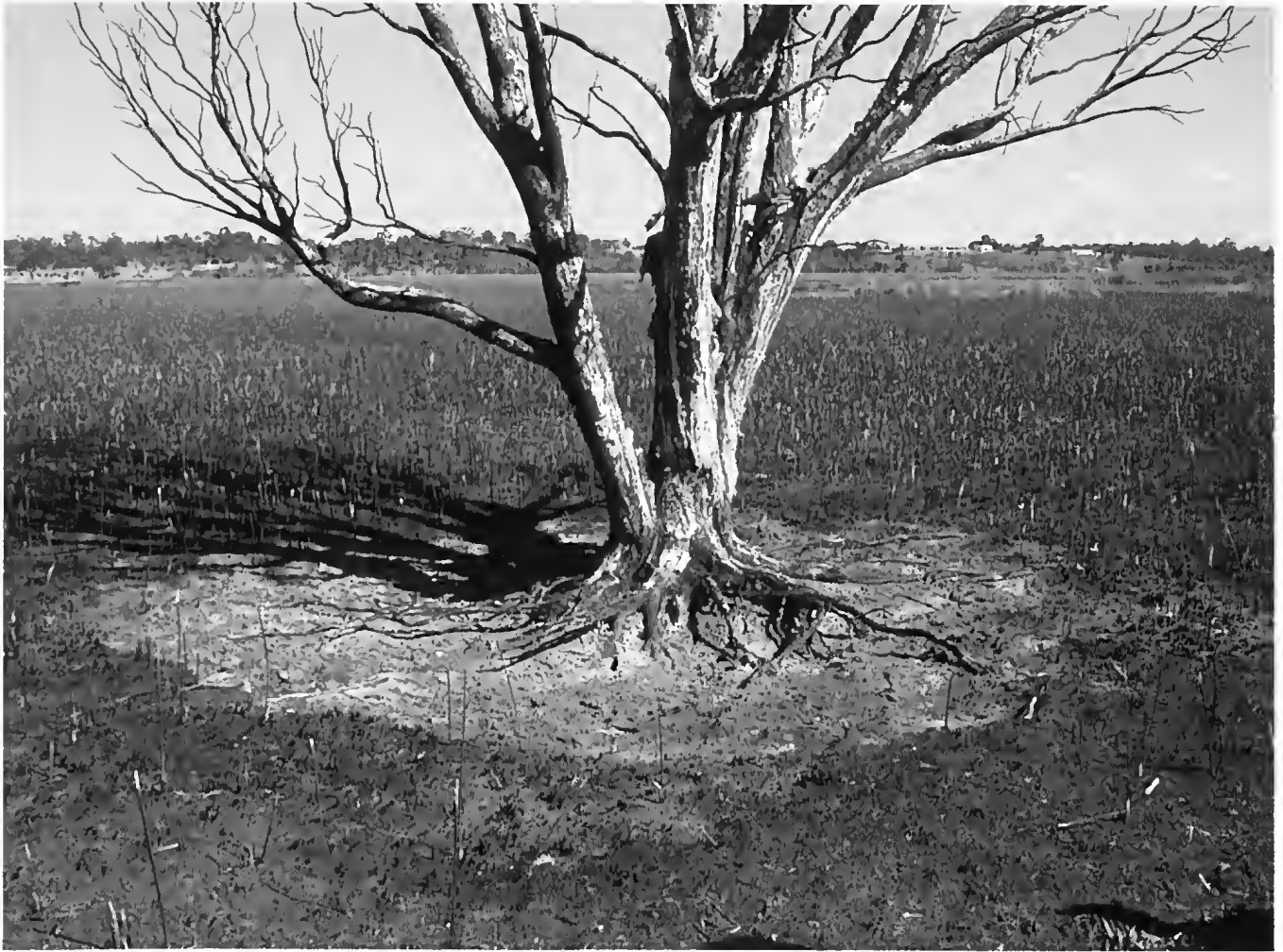
Figure 2. Burnt organic soils in Lake Mariginiup, Swan Coastal Plain, showing a circular depression up to 5 m wide where soil has been consumed to a depth of over 30 cm, exposing the roots of a *Melaleuca* sp. which has been killed in the process. Photograph J.M. Benier, 2003.

organic humic substances responsible for colour will precipitate with dissolved metals and phosphates, leaving the water colourless and low in phosphorus (see for instance Sommer & Horwitz 2001).

Of major concern in sulphidic sediments is the potential for heavy metals to be mobilized following oxidation, thereby contaminating surface waters. On the SCP, arsenic and aluminium in affected groundwaters have reached extremely high levels (Appleyard *et al*. 2004; Hinwood *et al*. 2005).

Trophic effects

For all aquatic habitats in well-vegetated catchments, it can be hypothesized that removal by fire of the shade and organic matter provided by riparian cover, and the removal of catchment leaf litter, may temporarily at least reduce organic matter input. Fire will expose those systems to more sunlight, elevated temperatures and greater levels of water column and overall wetland photosynthesis. The broader question has, therefore, focused traditionally upon the impact of changing fire regimes on the trophic dynamics in wetlands as they temporarily shift from heterotrophy to autotrophy.

From the catchment effects described earlier, increased nutrient concentrations, especially in conjunction with elevated pH, and increased light due to the removal of canopy by fire, leads to a rapid increase in productivity, usually by opportunistic algal species, with a potential for nuisance algal blooms. In some instances the inflow of nutrients and base cations might be beneficial to specific aquatic systems. Increased suspended sediments and turbidity can have a variety of impacts on aquatic organisms, including alteration of the light regime to which the biota has become adapted, smothering of aquatic plants and animals, and reducing the availability of oxygen.

In an acidification scenario, the combined effects of low pH (and associated metal toxicity), low nutrients and greater exposure to UV radiation can have an impact on aquatic communities. As well as being toxic for humans if ingested, high concentrations of these metals will have significant trophic effects in wetlands. For instance inorganic soluble ionic aluminium is toxic to fish, amphibians, macroinvertebrates, zooplankton, phytoplankton and algae, although a "toxic level" has not been defined (Schindler, 1988; Herrman, 2001). It is, however, difficult to differentiate between the effects of ionic Al and low pH (Herrman, 2001); in combination

they cause species reductions. Sommer & Horwitz (2001) noted significant changes in aquatic macroinvertebrate assemblages in a wetland on the Gnangara groundwater mound on the SCP (Lake Jandabup) affected by acidification. While the acidification was due, in this case, to drought and lowered water tables over a period of approximately 5 years, the net result may be similar to that of fire. There were 'local' extinctions of highly sensitive taxa such as amphipods (*Austrochiltonia*), mayflies (Caenidae) and planorbid gastropods; decreases in abundance of sensitive taxa such as ostracods and isopods (Amphisopidae); and increases in abundance of apparently acid-tolerant taxa (macrothricid cladocerans and the larvae of the sandfly Ceratopogonidae). Biogeochemical cycles in acidified waterbodies become disrupted as the microbial community is also affected by low pH. Whereas the effects of increased alkalinity and nutrient levels tend to be short-lived (see for instance Earl & Blinn 2000), recovery from acidification can be relatively slow, particularly if much organic matter were

lost from the wetland. Organic matter is required to reinstate reducing conditions and increase alkalinity by providing a substrate for microbes.

The effects of fire management on water quality

Water quality in wetland systems will respond to attempts to extinguish, or suppress, fire in the wetland or its catchment, as well as attempts to prevent fire from spreading into a wetland.

Fire suppression commonly uses retardant chemicals and fire suppressant foams. Hamilton *et al.* (1996) found that both fire-retardant and foam-suppressant chemicals were very toxic to aquatic organisms including algae, aquatic invertebrates and fish (see also Buhl & Hamilton 2000). They suggested that fire-control managers need to consider protection of aquatic resources from toxic effects, especially if endangered species are present.

Another technique considered for extinguishing fires in organic soils is flooding with water extracted or

Table 1

Summary of the effects of fire on water quality, showing four categories of effects, and the general consequences for water quality, their duration of change, and the trophic consequences, all derived from relevant literature. The last column summarises the hypothetical implications of this review for the situation on the Swan Coastal Plain.

Broad fire effects	Water quality responses	Duration of change	Trophic consequences	Implications for Swan Coastal Plain
Catchment effects (runoff, deposition)	Elevated base cations	Short term	Increased productivity	Highly localized only
	Alkalinity	Short term	Increased productivity	Highly localized only
	Elevated nutrient concentration	Short term	Increased productivity	Probable occurrence but magnitude of nutrient shift dependent on many factors
	Sediment input	Short and long term	Smothering, increased turbidity	Local smothering in littoral zone possible; turbidity change unlikely
	Groundwater recharge	Short term	Possible change to wetland surface water regime	Possible seasonal delay to recharge depending on intensity of burn and repellency of soil
Atmospheric effects of a fire in a catchment	Return to the ground of dissolved volatilized reactive and particulate compounds	Short term	Acidify wetland (change structure of aquatic communities)	Unlikely due to seasonal influences unless fires are followed by (intense) rain
Rehydration of burnt or overheated (organic) soils	Alkalinity Acidification -Lower pH -Water clarity -Loss of colour -Heavy metals	Short term Medium term to long term	Increased productivity Decreased in water productivity, altered structure of aquatic communities (loss of sensitive species, predominance of acid-tolerant forms).	Highly localized only Localized, potential for groundwater plume
Fire suppression effects	Toxic chemicals	Depends on half life of chemicals	Altered structure of communities, local extinctions	Probable assuming that response of local flora and fauna is equivalent to other taxa tested elsewhere
	Water movement	Long term	Introductions and potential extinctions	Information on sources of water insufficient to discuss implications
	Acidification from drainage/trenching /flooding	Medium term to long term	(see above)	(as above)
Fire Prevention Effects	(similar to catchment and atmospheric effects as above)	(as above)		

diverted from a nearby source. It is commonly reasoned that the potential for translocation of unwanted aquatic species, the accidental removal of endangered species (Jimenez & Burton 2001) or deleterious water quality changes, when water is moved via water carrying devices for fire suppression, are outweighed by the potential damage to wetlands from burning. As far as we can tell this reasoning has never been critically examined, and reliable data are required from south-western Australia to assess its validity.

As well as flooding, trenching has been applied to attempt to arrest the progress of burning peat in organic-rich soils in south-western Australia. When the flooding or drenching involves any digging of organic soils, or construction of trenches, the possibility is raised of exposing acid sulphate soils to aeration and developing a localized acidification event.

Where wetlands have significant ecological or cultural value, their protection using fire prevention methods involves the reasoning that reducing the biomass at the margins of a wetland will lessen the risk that a wildfire or an escaped burn will be able to be carried into that wetland. Whether this reasoning is sound or not, such prescription burns around wetlands will have at least the catchment, atmospheric and trophic implications for water quality as discussed in this paper.

General Discussion

Table 1 summarises the issues presented in this paper, and the implications of the findings for the organic- rich wetlands on the SCP. While the literature examined has been useful for framing categories of water quality response as above, we note that there have been no studies into the effects of fire on wetlands on the SCP in general, let alone the effects of fire on wetland water quality for this bioregion. Indeed fire, or a change in fire regime, are not mentioned by Davis & Froend (1999) in the context of disturbances to wetlands, and fire as a process is only briefly mentioned in Balla's (1994) otherwise comprehensive treatise on management issues for wetlands on the SCP.

The literature shows that fire regime in catchments certainly has implications for water quality. The question of the effects of fire intensity and seasonality on soil water repellency and thereby for recharge into unconfined aquifers, and runoff into wetlands, emerges as a critical one for managers of the city of Perth's water resources and wetlands on the Plain.

A conundrum was raised by Horwitz et al. (2003): why are organic soils burning more often in recent times when they should be persistently damp even during dry seasons or drought, and thereby able to resist the passage of a fire? This suggests either a fire regime change, or organic soils are drying out more than previously, or both. Declining rainfall and anthropogenic effects such as groundwater abstraction for domestic and horticultural purposes are undoubtedly rendering organic soils on the SCP drier than they have been for significant period of time (perhaps even thousands of years). Such drying results in a vulnerability to fire, particularly if more intense fires occur in what have become seasonally inappropriate times (any time from

the period late spring to late autumn). The simultaneous occurrence of drought and fire is likely to increase on the SCP, as it is elsewhere (Hogenbirk & Wein 1991). A likely prognosis will be for fires to occur in organic soils until they resume their seasonal and yearly moisture levels, and/or until fire regimes, including arson attacks during hot periods, change.

The potential consequences for water quality of fire suppression and fire prevention demonstrate that fire management cannot rely on single approaches or quick fix solutions for fire in wetlands. Management should therefore apply a precautionary approach to prevent irreversible losses (like erosion of organic soil profiles) and otherwise use an adaptive management framework that will include testing the hypotheses stated herein.

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A review of biodiversity in wetlands with organic sediments on the Swan Coastal Plain, Western Australia, with an emphasis on aquatic invertebrates

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Abstract

Wetlands on the Swan Coastal Plain with sediments composed largely of organic matter include those with soft oozes, largely derived from decaying phytoplankton, and those with coarser peaty sediments derived from vascular plants. The former appear to have a flora and fauna very similar to wetlands with mineral dominated sediments. Peat deposits on the Swan Coastal Plain are not common but occur where permanent moisture, during past or present climatic regimes, has allowed production of plant material to exceed decomposition. Active peat deposition is largely restricted to *Baumea* and *Melaleuca* dominated swamps and a small number of mound springs. These wetlands tend to support species of aquatic invertebrates that are rare or absent elsewhere in the region and which frequently represent outlier populations of species more common in less xeric regions. This is also true of some plant species occurring on the mound springs. Fire can dramatically alter such wetlands when it burns the organic sediments and poses a threat to their biota.

Keywords: peat, biodiversity, aquatic invertebrates, Swan Coastal Plain wetlands

Introduction

All wetland sediments contain organic matter, derived from dead and decaying animals and plants. Under certain conditions, generally involving low oxygen concentrations in permanently moist situations, this material accumulates faster than it decomposes and can come to compose almost the entire wetland bottom, sometimes to a depth of several metres (Clymo 1983). Organic sediments of Swan Coastal Plain (SCP) wetlands range from fine silty oozes of deeper lakes derived from phytoplankton production settling out on the lake bottom to that formed by coarser organic matter, usually called peat. The peat is derived from decaying vascular plant material that accumulates in shallow swamps or in stands of sedges fringing open lakes (herbaceous peats *sensu* Kivenen 1977). A particular type of peat-based wetland on the Swan Coastal Plain are the mound springs that occur along the eastern edge of the Bassendean Sands that have formed due to localised peat build-up around groundwater discharge points at the boundary between the permeable Bassendean Sands and the impermeable Guildford Clays (Knott & Jasinska 1998). Active peat deposition is otherwise largely restricted to wetlands with dense stands of *Baumea* but substantial peat deposits are rare on the SCP. Semeniuk & Semeniuk (2005, this issue) provide a review of the extent and formation of organic wetland sediments in the region. Wetlands with organic sediments, especially those with peat sediments, are often characterised by coloured water, low pH, low productivity, dense vegetation, shade, shallow depths and perennial moisture (albeit subsurface moisture where surface water

is only present seasonally). These characteristics, probably more so than the immediate effects of the physical presence of organic matter, influence the composition of the biota and can lead to biological communities that are distinct from those in other types of wetlands. The summer drying of surface sediments in many of these wetlands makes them prone to fire, resulting in loss of organic matter and other chemical and physical changes (see Horwitz & Sommer 2005, this issue).

The following review of biodiversity in organic wetlands of the Swan Coastal Plain was produced for a workshop on Preventing Burning in Organic Wetlands organised by Edith Cowan University and Fire and Emergency Services Association. I will concentrate on the aquatic invertebrates and provide brief comment on some aspects of the flora and waterbirds, although terrestrial and edaphic invertebrates are also likely to be diverse and to show some association with humic soils around wetlands.

Aquatic invertebrates

A recent review of aquatic invertebrates recorded from the Swan Coastal Plain identified 332 taxa (Horwitz, unpublished manuscript), some of which are likely to represent multiple species (e.g., unidentified nematodes, copepods, water mites and some dipteran families). In addition, while rotifers represent 15–20 % of invertebrates present in other regions of WA (Halse *et al.* 2000; Pinder *et al.* 2004) they have received virtually no attention on the Swan Coastal Plain. Some other microinvertebrates, such as chydond cladocerans are also poorly surveyed. This, and the fact that a relatively small number of wetlands have been thoroughly surveyed,

suggests that the number of species inhabiting the region's wetlands is likely to be in excess of 500. However, few of the known species are restricted to the Swan Coastal Plain and only about 15 % are even endemic to south-west Western Australia (P. Horwitz, Edith Cowan University, unpublished manuscript).

The most comprehensive study of wetland invertebrates was undertaken by Davis et al (1993) and aimed, in part, to classify SCP wetlands on the basis of their invertebrate fauna and to relate patterns of invertebrate occurrence to environmental variables. A cluster analysis of wetlands based on invertebrate community composition produced several groups of wetlands, including one consisting primarily of coloured and/or seasonal wetlands. Colour of the water (due to dissolved humic substances), hydrological seasonality, pH, nutrient concentration and salinity were all correlated with invertebrate community composition. Some sediment organic content data was collected by Davis et al (1993) but were not used in their analyses and could not be sourced for this workshop. However, peat-based wetlands tend to be seasonal and to have coloured waters with low pH, more so than wetlands with fine lacustrine organic sediments (mud, organic ooze and periphyton) or mineral sediments, so are likely to contain a distinctive, though variable, suite of species. In the study by Davis et al (1993), no species were restricted to coloured seasonal wetlands but some, such as the copepod Calamoecia attenuata and an oribatid water mite were more likely to occur in such wetlands than elsewhere. Some open lacustrine wetlands, such as Lakes Goolellal and Thomson, have sediment with moderately high organic content (Davis et al., 2003). However, there is little evidence that they have invertebrate faunas distinct from otherwise similar wetlands with mineral sediments. The following discussion is thus restricted to the more peat-based swamps and springs. More recent studies of peat swamps and mound springs have shown that some have unusual elements in their invertebrate faunas, including species that are otherwise rarely recorded on the SCP and some which appear to represent northern outliers from more mesic south-west distributions.

A survey of invertebrates of Lake Tamworth, a sedge swamp with deep (>1 m) peat sediment near Baldivis, undertaken as part of an impact statement for a peat mining proposal, found 48 species of macroinvertebrates, most of which are common on the Swan Coastal Plain and occur in other types of wetlands (Streamtec Pty Ltd 1991). Exceptions were the caddisflies Ecnomina sentosa (Ecnomidae) and an unidentified species of Philopotamidae. These insects, typical of streams in the Jarrah Forest and far south-west, have not been recorded elsewhere on the SCP, other than one record of the E. sentosa from a river near Busselton (Sutcliffe 2003), so their presence in this swamp needs to be verified. An acidic coloured swamp in Melaleuca Park on the Gnangara Mound near Bullsbrook, with a less substantial layer of peat (< 10 cm) overlying peaty sand (to 20 cm), is home to a population of the Black Striped Minnow (Galaxias nigrostriata) (Knott et al 2002). This is 350km north of its main area of distribution: between Augusta and Albany where it also inhabits acidic peat swamps (Morgan et al 1996). Its persistence at this site was

attributed to the highly coloured water which allowed cool temperatures to persist at depth (< 16° C during the day in late spring 1995) and the presence of a spring which kept a small part of the wetland permanently moist during summer. Knott et al (2002) also found numerous chydorid cladocerans at this site, including a species of Rak. The latter was originally identified as Rak obtusus, believed at the time to otherwise only occur in similar habitats near Northcliffe in WA and in eastern Australia. However, the Northcliffe specimens are now known to be an undescribed species and the Melaleuca Park Rak could be different again since two other undescribed species are known from south-west WA (R Shiel, Adelaide University, pers. comm.). The genus has not been reported from elsewhere on the SCP but few studies have reliably sampled microcrustacea in the region.

The peat-forming mound springs on the eastern edge of the Gnangara groundwater mound are listed as a Threatened Ecological Community (English & Blyth 2000) under the Commonwealth Environment Protection and Biodiversity Conservation Act 1999. This recognition is largely based on their aquatic invertebrate communities. Two of these, plus several other springs (some of which also had peat deposits at their discharge points), were sampled by Jasinska & Knott (1994). These were found to have diverse and heterogenous invertebrate assemblages: the total of 147 species included 84 that occurred in the springs with peat and 54 found only in such springs. Jasinska & Knott (1994) indicated that some of the species occurring in the peaty springs had not been recorded in other SCP wetlands and there appeared to be a particularly high diversity of copepods (including Paracyclops spp. which appear to be uncommon in lacustrine wetlands of the SCP). Unfortunately, taxonomic impediments, including a lack of consistent morphospecies coding between research groups, prevent detailed comparisons with other SCP studies. Some, such as the ostracod attributed to Darwinula (this genus has since been revised and split into several genera), may be widespread in the source groundwater aquifer. Jasinska (1998) and Pinder (2003) added to the species lists for the mound springs (including one not sampled previously), recording new species of water mites (including the first WA records of Anisitellidae and a new genus of Aturidae) and the hydrophilid beetle Coelostoma ?fabrieii, which is uncommon on the SCP. Two species of dragonflies collected from these springs are also rare on the SCP but relatively common in the Jarrah Forest and Warren regions (Sutcliffe 2003): Archaeosynthemis ?leachi which inhabits permanent streams, boggy seepages and swamps and Austrogomphus lateralis, which mostly inhabits permanent streams and swamps (Watson 1962; Sutcliffe 2003). Similarly, Ecnomina sp. AV18, was collected from one of these springs but is otherwise known only from peaty swamps of the southern Darling Range, Warren region and south-coast (Sutcliffe 2003). The mosquito Culiseta atra, which most frequently occurs in coloured standing water bodies with decaying vegetation, also occurs in these springs but not in more open lakes of the SCP.

Similar organic mound springs on the western slopes of the Dandaragan Plateau near the town of Three

Springs have also been shown to have populations of invertebrates, including the dragonfly *Archaeosynthemis occidentalis,* an undescribed chironomid (non-biting midge) and two phreodrilid oligochaetes, that otherwise occur much further south (Pinder 2002; Pinder & Pennifold 2002) and to have communities unlike those found in other wetland types of the region (Pinder *et al.,* 2004). *Culiseta atra* also occurs in these mound springs, well north of other published populations. These springs are also recognised as a Threatened Ecological Community (recovery plan in preparation) and are prone to damage by fire.

In summary, vegetated swamps and springs with peat deposits provide habitat for a range of aquatic invertebrates that appear to be uncommon or absent in other types of wetlands on the SCP, though more survey work is required to document the extent of this. In particular, the aquatic microinvertebrate fauna (rotifers, ostracods, copepods and cladocerans) is poorly surveyed on the SCP. These groups are turning out to be very diverse and endemic in south-western Australia, with numerous new species being described from dystrophic and/or ephemeral wetlands of the far south-west (e.g., Frey 1991; Segers & Shiel 2003). Similar wetlands of the Swan Coastal Plain may also contain undescribed microfaunal diversity.

Waterbirds

All 116 waterbirds known from south-western Australia have been reported from the SCP. A quantitative survey by Storey *et al* (1993) recorded 79 species and found that those SCP wetlands with high richness and abundance of waterbirds tended to be the deeper, larger wetlands with high productivity, low colour and plenty of fringing emergent vegetation. Sediment characteristics were not measured in that survey but peat wetlands are generally not characterised by these correlates of high waterbird usage. In particular, peat swamps are generally not productive enough to provide sufficient food resources for rearing young and many are shallow with little open water so are unsuitable for supporting large numbers of ducks. Halse *et al* (1993) found many waterbirds to be positively associated with deep permanent wetlands but few associated with shallow seasonal wetlands in south-western Australia. Several species were positively associated with extensive sedges, including bitterns (Australasian and little), crakes (Baillon's, spotted, spotless), musk ducks, purple swamphens, reed warblers and little grassbirds. These species are particularly likely to be associated with vegetated peat swamps of the SCP.

Flora

Of the wetlands with active peat deposition on the SCP, the mound springs have the most interesting plant communities. These wetlands, dominated by *Melaleuca rhaphiophylla* over sedges, especially *Cyathochaeta teretifolia*, have now mostly dried up or have been excavated (to create farm dams) or have been cleared of vegetation (English & Blyth 2000) and some have been damaged by fire. These are mostly recognised as a

Threatened Ecological Community for their distinct invertebrate fauna, but the three remaining occurrences also contain a number of plant species that are either highly disjunct or are south-west WA or Darling Range species that are otherwise uncommon on the SCP.

Examples include several liverworts (e.g., *Gleobelobryum ungriculatum)*, ferns and fern allies *(Cyclosorus interruptus* and *Lycopodiella serpentina)*, orchids *(Corybas dilatatus)*, sedges *(Cyathochaeta teretifolia* and *Empodisma gracillimum)*, shrubs *(Hibbertia perfoliata* and *Boronia molloyae)* and trees *(Homalosperinum firmum)*. *Hibbertia perfoliata* was presumed to have become extinct on the SCP until found on these mound springs recently. These mound springs are prone to fires, especially in dry years, destroying the peat and allowing weed invasion. Extraction of water from the Gnangara Mound may acerbate this threat if the hydrology of the springs is affected.

Accumulation of coarse organic material also occurs in swamps dominated by *Baumea* sedges but, unlike the mound springs, these wetlands do not seem to support plant species that are particularly rare on the SCP or outside of their core ranges.

Conclusions

Most plant and animal species that inhabit wetlands with peaty sediments of the SCP are widespread and occur in other types of wetlands on the plain and usually elsewhere. However, for a range of species that are otherwise rare or absent on the SCP, such wetlands provide moist refuges in a generally xeric region. These are mostly species whose distributions are otherwise either broad but disjunct or centred on more mesic parts of the south-west. Fire can destroy the organic sediments and lead to significant changes to the physical and chemical nature of peat-based wetlands and is thus a significant threat to their biodiversity and to the continued occurrence of numerous individual species on the SCP.

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Potential health impacts associated with peat smoke: a review

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Abstract

In Western Australia, peat is distributed throughout the Swan Coastal Plain, in the South West and North West regions of the State. Peat is typically associated with wetlands and its distribution has significantly reduced over the past 100 years. The major threats to the current distribution of peat are fire and land use changes. Peat is thought to be at increased risk of fire in particular due to the proximity of residential development and the drying period being experienced in South Western Australia. Peat, largely arising from accumulated plant matter, burns very easily when dry and fire in these systems is often very hard to extinguish due to the depth of material. Peat smoke is made up of a complex mixture of water vapour, gases and fine particles. In general, peat smoke is characterized by high concentrations of organic carbon, elemental carbon, and potassium. The gases in peat smoke include carbon monoxide, carbon dioxide, nitrogen oxides, sulfur oxides, carbonyl compounds, polycyclic aromatic hydrocarbons and other irritant and hazardous volatile organic compounds. All of these have been shown to cause deleterious physiologic responses at high concentrations in laboratory studies of animals and a limited number of chamber studies of humans at lower concentrations. There is little known about the health effects of exposure to peat smoke as few studies have focused specifically on this potential source of air pollution. Information is, however, available on the composition of peat smoke and there are some studies arising from specific fires which resulted from burning of underground environments, including events in Russia, USA and Indonesia. Peat smoke therefore represents a concern for communities living in areas where there is an increased risk of fire and where duration of fire in these systems is lengthy.

This paper presents a review of information available on adverse health effects, notably respiratory diseases and symptoms, associated with components of peat smoke. The health effects reported from epidemiological studies from which exposure to peat fires has been referenced is also reviewed, along with a summary of some of the literature on exposures to bushfire smoke which shares similar components to peat smoke.

Keywords: peat smoke, health, smoke composition

Introduction

Peat is characterized by the presence and accumulation of decaying plant material or organic matter (Ryder 2000). When it is dry, it burns very easily producing smoke. Peat is unique in the way it burns as the heat generated can facilitate fire moving through the soil profile resulting in fires lasting for extended periods lasting for days to months (Hungerford *et al* 1996; Kirk 2002). Peat fires are hard to extinguish due to the fact that fire follows the layers of peat as far as fifteen meters into the earth (Hungerford *et al*. 1996; Kirk 2002). One of the problems of burning forests to clear land is the potential for ignition of fires in outcrop deposits of coal or peat, which can then smoulder underground for many years and re-igniting again given appropriate conditions (Hamilton *et al* 2000). The widespread fires throughout the forested peat lands of Indonesia during 1997 is an example of where deforestation and subsequent fire resulted in the ignition of peat with smoke being produced for months. In Indonesia, Page *et al* (2000) reported that on the Borneo island in Central Kalimantan, 32 % of the area burned was peat and accounted for 91.5 % of the burned material.

Peat fires are characterized by significant quantities of smoke and emissions of which carbon dioxide is a significant component. However, the nature of the pollutants released during peat fire varies according to the composition of the peat, the geology of the area, the depth of the fire and the temperature achieved. Such variables will influence the composition and concentration of smoke components and therefore the potential for health impacts. In addition to the smoke composition, the degree of exposure to smoke by individuals and communities, their health status and the duration of exposure will also influence the potential for adverse health outcomes.

Peat is widely distributed on the Swan Coastal Plain, although there is an estimated seventy percent loss of the original extent due to past land use practices and urban development (Davis & Froend 1999). The remaining peat deposits are under pressure particularly from continued urban development and fire.

With the proximity of residential development to peat deposits, a drying climate and the associated risk of fire, the potential for human exposure to peat smoke exists. If

fires occur for extended periods, exposure to smoke and smoke components may also be prolonged.

This paper provides a review of the available literature on the health effects of peat from studies of smoke and peat fires. Use is made of the literature pertaining to bushfires due to the small number of studies reporting health effects associated with burning of peat and the presence of similar compounds in bushfire smoke which have been associated with health effects.

Peat Fire Smoke Composition

Peat smoke is a complex mixture characterized by high concentrations of organic carbon, elemental carbon, potassium and sulphur (Ramadan et al. 2000; Gebhar et al. 2001). Peat burning produces many other potentially harmful gases and combustion by-products, including fine particles (Itkonen & Jantunen 1983; NCDENR 1998). Both PM10 (coarse fraction, with particle diameter < 10 µm) and PM2.5 (fine fraction, with particles diameter < 2.5 µm) have been found in the smoke arising from peat fires with PM2.5 being the predominant fraction (Joseph et al 2003). Peat-fire smoke also contains ammonia which reacts with oxides of nitrogen and sulfur to form fine particles (PM2.5) (Breas et al 2001; Anderson et al 2003).

The gases produced in peat fires include carbon monoxide, carbon dioxide, nitrogen oxides, sulfur oxides, aldehydes, polycyclic aromatic hydrocarbons and other irritant volatile organic compounds (VOCs) (Itkonen & Jantunen 1983). Page et al (2002) estimated that in Indonesia in 1997, 0.81 to 2.57 Gt of carbon were released to the atmosphere as a result of burning peat and vegetation. This is equivalent to 13–40 % of the mean annual global carbon emissions from fossil fuels, and contributed greatly to the largest annual increase in atmospheric CO_2 concentration detected since 1957 (Page et al 2002). In Russia in 2002, fires emerged across West Russia. Satellite analysis estimated a burned area of more than eleven million hectares of land with the resulting haze reducing visibility in Moscow. Carbon dioxide was measured at three times its usual concentrations (Kirk 2002).

In the 1997 Indonesian forest fires, the particles emitted contained high sulphur to potassium (S/K) ratios. These high ratios originated from the sulphur dioxide (SO_2) released through the combustion of peat below the ground (Ikegami et al 2001) The particle emissions from savannah fires in southern Africa also have high S/K ratios from fine particulate samples (Liu et al. 2000). Peat fires in the Amazon bush were found to contain potassium, chlorine and sulphate dominated PM2.5, while calcium and acetate dominated the coarse fraction (Allen & Miguel 1995). In general, savannah and tropical forest biomass burning could be responsible for the emission of about 1 Gg yr^{-1} of copper, 3 Gg yr^{-1} of zinc and 2.2 Tg yr^{-1} of black carbon to the atmosphere (Yamasoe et al 2000).

Polycyclic aromatics and dioxin-like compounds have been measured in the smoke from peat fires. In Indonesia in 1997, concentrations of polycyclic aromatic hydrocarbons in areas affected by smoke were 6–14 times higher than levels in unaffected areas (Kunii et al 2002). Very low concentrations of dioxin-like compounds

(polychlorinated dibenzo-p-dioxins (PCDD) an dibenzofurans (PCDF), non-ortho polychlorinated b phenyls (PCB) and mono-ortho PCB) are reported to aris from burnt vegetation and burnt soil (Martinez et a 2000). Some authors consider that the main contributio to dioxin emissions is by firewood and peat combustio through incomplete combustion of organic carbon in th presence of chlorine (Kakareka 2002; Perkins 2003).

Other hazardous substances released during pea burning include methyl chloride, non-methan hydrocarbons, ethylene, volatile organic compound (VOC), methyl bromide, benzene, polynuclear aromati hydrocarbons and their oxygenated derivatives. Selecte VOCs and methyl bromide play an important role i ozone depletion (Keppler 2000) while benzene polynuclear and polycyclic aromatic hydrocarbons ar reported carcinogenic substances (McCauley et al 199 Keppler et al. 2000; Kjallstrand & Petersson 2001; Wipp et al 2001; Czapiewski et al 2002; Tsapakis et al 2002).

There are a number of other substances found in pea smoke. Fires can mobilize radionuclides fror contaminated biomass through suspension of gases an particles in the atmosphere or solubilization an enrichment of the ash (Amiro et al 1996). In a study c peat combustion, field and laboratory experiments wer conducted to determine the fate of iodine (I), cesium (Cs and chlorine (Cl) in biomass fires (Amiro et al 1996 During a typical field fire, 80–90 % of the iodine an chlorine, and 40–70 % of the cesium were lost to th atmosphere, the remainder being left behind in the as in a soluble form. The authors consider that if th elements were radioactive isotopes, such as [129]I, ^{137}Cs an [36]Cl, fires could cause an increased radiological dose t people through inhalation, exposure to ash, or ingestio of plants because of increased uptake of ash leachat (Amiro et al 1996). In Sweden in 1983, high uraniur concentrations were observed in peat ash with externa gamma radiation dose rates up to 10 microGy/h (Ehdwa et al 1985).

Potential Health Impacts of Peat Smoke Exposure

The concentration of pollutant, extent and duration c exposure, age, individual susceptibility and other factor play a significant role in determining whether or no someone will experience smoke-related health problems

Several epidemiological studies have been conducte as a result of smoke originating from peat fires the mos significant being the Indonesian forest and peat fires c 1997 (Emmanuel 2000; Hamilton et al 2000; Ikegami et a 2001; Page et al 2002).

In June 1997, mainly in the Kalimantan and Sumatr islands, more than 1,500 fires consumed more tha 300,000 ha of forests, and generated intense smok affecting neighbouring countries (e.g., Singapor Malaysia, Thailand) and the Indonesian Islands fo several months. The local health impact of the Indonesia fires has not been well documented although increases i hospital admissions for respiratory problems have bee reported in Singapore (Emmanuel 2000).

Following acute exposure to air pollutants fror Russian forest and peat bog fires in 2002, healt

authorities reported an increase in the number of reports of acute symptoms such as headaches, watery eyes and tiredness (Kirk 2002). Other acute symptoms reported after exposure to peat fire in Craven County, North Carolina included dizziness, weakness, sleepiness, nausea, vomiting, confusion and disorientation (NCDENR 1998).

Several large wildfires and peat fires occurred in Florida during June-July 1998. A survey of selected diseases was conducted in 8 hospitals to determine whether certain medical conditions increased in frequency during the wildfires compared with hospitalisations during the same period in the previous year. From 1997 to 1998, the emergency departments (ED) visits increased substantially for asthma (91 %), bronchitis with acute exacerbation (132 %), and chest pain (37 %) (MMWR 1999).

Health Effects of Specific Components of Peat Smoke

Information is available on the health effects of some of the individual components of peat smoke which are also components of bushfire smoke. Many studies report associations between individual components such as particulates or nitrogen dioxide due to the complexities of assessing the health effects of mixtures such as smoke arising from bushfire or peat fires. Many of the components of peat or bushfire smoke are also found in emissions from industry and motor vehicles and have been associated with a variety of health effects.

Particulate Matter (PM): Particles which may be produced from peat fires are considered harmful to health when the results from studies of particles arising from other sources are considered (Pope & Dockery 1992; Li *et al* 2003). PM10 and PM2.5 particles can be inhaled into the lungs causing lung irritation, damaging lung tissue and causing respiratory and cardiovascular problems (Pope 1996; Joseph *et al* 2003). People with heart disease, like congestive heart disease, might experience chest pain, palpitations, and shortness of breath or fatigue following exposure to particulate matter. People with lung conditions such as chronic bronchitis, chronic obstructive lung disease, emphysema and asthma may not be able to breathe as deeply or as vigorously as usual, and they may experience symptoms such as coughing, phlegm, chest discomfort, wheezing and shortness of breath. (Larson & Koenig 1994; Joseph *et al* 2003). The deposition of particles in the lung induces a systemic inflammatory response detected by increased levels in cytokines. (van Eeden *et al* 2001).

Fine PM has been associated with increased morbidity and mortality among individuals with cardiovascular disease and can aggravate chronic heart and lung diseases (Pope 1996; Hong *et al* 1999; Joseph *et al* 2003). Fine particle matter has been linked to premature deaths in people with these conditions (Burnett *et al* 1998; Hong *et al* 1999; Joseph *et al* 2003). Some studies report that PM may exacerbate asthma and cause coughs and other respiratory symptoms in children (Pope & Dockery 1992; Gauvin *et al* 2002). In addition, prolonged exposure to PM may also affect the growth and functioning of children's lungs producing decreased pulmonary

function, increased respiratory symptoms, increased lower respiratory infection and increased chronic lung disease (Larson & Koenig 1994; Gauderman *et al* 2002; Horak *et al* 2002). This may be important if exposure to peat smoke occurs at an important development stage for children.

In asthmatics, epidemiological studies generally show a positive relationship between the particulate fraction of air pollution and increased morbidity (Goldsmith & Kobzik 1999). The Australian National Environment Protection Council (NEPC) suggests that each increase of 10 $\mu g/m^3$ in the ambient concentration of fine particulate is associated with a 3.0 % increase in asthma exacerbations (NEPC 2000).

Carbon Monoxide: Carbon monoxide (CO) is one of the most important components of smoke from peat fire which can pose a health hazard at high concentrations (NCDENR 1998). CO has been associated with increased respiratory and cardiovascular mortality (Hexter & Goldsmith 1971; Burnett *et al* 1998; Hong *et al* 1999). The health effects associated with exposure to CO range from the more subtle cardiovascular and neurobehavioral effects at low concentrations to unconsciousness and death after acute or chronic exposure to higher concentrations of CO. Symptoms include headache, dizziness, weakness, nausea, confusion, disorientation, and visual disturbances and severe poisoning results in marked hypotension, lethal arrhythmias, and electrocardiographic changes (NCDENR 1998; Raub *et al* 2000; Kirk 2002).

People with angina or heart disease, pregnant women, developing fetuses, and those who exercise outdoors are particularly sensitive to carbon monoxide pollution (NCDENR 1998). Neurological effects of acute CO poisoning includes disorientation, confusion, and coma. (Raub *et al* 2000). The effects can range from mild, annoying symptoms relieved by removal of the source, to severe morbidity with profound central nervous system dysfunction and acute complications (Abelsohn *et al* 2002).

Sulphur dioxide: Increases in hospital admissions for respiratory diseases, particularly asthma, have been associated with elevated concentrations of SO_2 (Guillen *et al* 1995; Brown *et al* 2003). Chronic exposure to PM and SO_2 is associated with up to three-fold increases in non-specific chronic respiratory symptoms in children and long-term outdoor winter concentrations of SO_2 has been associated with wheezing/whistling and with asthma diagnosed by a doctor (Pikhart *et al* 2001). Asthmatic children are susceptible to increased levels of SO_2, even with ambient levels considered within "acceptable" ranges (Chew *et al* 1999). In a case control study of the risk of hospital admission for chronic bronchitis, an increase of 10 % resulted from a 10 ppb increase in SO_2 concentration (in the range 0–60 ppb) (Ciccone *et al* 1995). A similar positive association was observed for exposures to more than 10 ppb of SO_2 and hospitalization for ischemic heart diseases (Ciccone *et al* 1995).

Health effects of exposure to wildfire or bushfire smoke

During the last few years there have also been a

number of fires involving exposure of large populations to air pollutants from large uncontrolled fires burning in underground and coal surfaces in countries including China, India and Indonesia. This information can be used to make some inference about the potential health impacts that may be associated with exposure to peat smoke.

Direct exposure to bushfire smoke has been linked to increases in a variety of community respiratory problems. Symptoms from short-term smoke exposure can range from throat irritation, cough, irritated sinuses, headaches, runny nose and eye irritation to more serious effects in persons with asthma, emphysema, heart disease and other existing medical conditions (Kunii *et al.* 2002; Emmanuel 2000; NCDENR 1998).

Duclos *et al* (1990) assessed hospital emergency room attendance in six counties arising from the California forest fires of 1987. They found an increase in the number of visits of persons with asthma, chronic obstructive pulmonary disease, sinusitis, laryngitis and upper respiratory infections were increased however no statistical increase in hospitalisations was observed (Duclos *et al* 1990). Mott et al (2002) assessed the health effects of the Californian fires of 1991 and again found increased visits to hospital for respiratory illness of 57 % compared with the previous year.

Between September 1997 and November 1997 in Indonesia, there were 527 haze-related deaths, 298,125 cases of asthma, 58,095 cases of bronchitis, and 1,446,120 cases of acute respiratory infection reported (Kunii *et al* (2002). In South Sumatra, the number of acute respiratory infection cases increased 3.8 times during the aforementioned time period, compared with the previous year. Ninety percent of 543 people interviewed about acute symptoms reported respiratory symptoms, and the elderly reported an overall deterioration of health. Gender, being older, and having a history of asthma was associated with an increased severity of respiratory problems (Kunii *et al* 2002).

In Singapore, the impact of the 1997 Indonesian forest fires was felt as a result of the prevailing winds. Emmanuel (2000) studied the potential health effects of the daily measured concentrations of the five major air pollutants: sulphur dioxide, particulate matter (PM10), nitrogen dioxide, ozone and carbon monoxide. The authors found a 30 % increase in outpatient attendance for haze-related conditions. An increase in PM10 levels from 50 microg/m^3 to 150 microg/m^3 was significantly associated with increases of 12 % of upper respiratory tract illness, 19 % asthma and 26 % rhinitis. Sizing of the haze particles showed that 94 % of the particles in the haze were below 2.5 μm in diameter (Emmanuel 2000). During the same period, there was also an increase in accident and emergency attendance for haze-related conditions, however there was no significant increase in hospital admissions or in mortality despite particulate levels being substantially higher than usual levels, possibly explained by differences in the particle size distribution during this particular bushfire (Emmanuel, 2000).

In Australia, Johnston *et al* (2002) investigated the relationship between bushfire smoke and emergency attendance at hospital for asthma. The authors of this study considered data from the dry season when bushfire activity is high and found that ED attendance increased significantly on days when PM10 concentrations were above 40μgm^3 compared with days below 10 μgm^3 (Johnston *et al.* 2002).

Studies of the Sydney bushfires have not demonstrated relationships between a variety of health outcomes (Jalaludin *et al* 2000; Smith *et al* 1996).

Concluding Remarks

The specific relationship between peat smoke and health effects has been identified as being of concern but is not well documented. It is clear that peat fires contribute smoke and component air pollutants that have been associated with adverse health impacts in toxicological and epidemiological studies. Additional studies are required to understand the potential health impacts of prolonged or repeated exposures to peat smoke and whether the composition of peat significantly impacts on a variety of health outcomes.

What makes peat fires of concern is the resultant smoke and duration with which they burn, significantly increasing the health risks associated with such fires. There is the possibility of long term health implications depending on the duration of the fires, the composition of the peat, the temperature of the fires and the health status of those exposed. The on-going investigations arising from the Indonesian fires for example, need to be monitored so the potential risks can be further considered.

The potential for health impacts needs to be taken into account when considering the role of fire and peat. Public health professionals have an important role in informing and educating vulnerable communities about the acute and possible long health effects of peat smoke exposure.

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Peat Fires: the dangers from a Fire Manager's point of view

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Abstract

Based on the experiences of the personnel of the Fire and Emergency Services Authority who have attended number of peat fires on the Swan Coastal Plain in recent years, it has become evident that firefighters have to confront specific dangers and logistic difficulties associated with managing such fires in regard to access, environmental considerations, and the possibility of injuries. Generally, each fire has presented significant issues associated with fire suppression, recall to the fire, environmental consequences and the potential poor air quality that affects local communities. Once alight peat fires can take much longer to suppress than normal surface fires, and they are very complex events that require careful planning and management, as well as coordination across various agencies including local government.

Keywords: peat fires, safety, health, access, fire management

Introduction

Over the past decade, lake systems and surrounding low lying areas in and around Perth and the Swan Coastal Plain, generally, have exhibited extended periods of decreased water levels, and as the water levels have dropped, peat has been exposed and the possibility of fires involving peat has increased. While some fires have been triggered by lightning, there also has been an increase in peat fires due to increased arson and the subsequent lighting of stolen cars in wetlands (Fig. 1). Firefighters are now having to more and more face the complexity of how to deal with peat fires, a situation further complicated when these fires are in close proximity to residential areas, and fire managers must now develop best practice management strategies on how to deal with such fires.

This paper briefly summarises the general issues associated with peat fires from a management perspective; these range from the extended period that peat may burn, to issues of access, safety and health, the extinguishing of peat fires, and the possibility that such fires may become the source of secondary bush fires long after the original ignition of peat. The paper also describes some aspects of specific bush fires (such as the one at Neerabup, or the fire at Lake Carabooda).

This paper draws on my personal experiences of fire management on the Swan Coastal Plain and presents some opinions and discusses imperatives for fire management in peat soils

Issues for managing fires in peat

There are seven issues in managing peat fires; these are: (1) peat burning for extended periods; (2) access to the fire; (3) methods of extinguishing the fires; (4) safety for the firefighters; (5) community health and safety; (6) the burning of peat being the source of a second fire; and (7) incident management and reporting for circumstances where peat is ignited.

Peat burning for extended periods

Once alight, peat can burn for extended periods well beyond the passage of the fire front, and peat fires are frequently more difficult to extinguish than those deriving from standard surface fuels. In some areas around the world, where the peat is deep and extensive, it has taken years to be sure that a peat fire is extinguished. However, if such fires are not extinguished there is a risk that the smoldering substrate will be the catalyst for an escape into un-burnt areas. Regardless of whether a decision is made to either extinguish or isolate the peat fire area, it will be necessary for firefighters to access the area, and be appropriately prepared for peat fire management.

Figure 1. A dumped vehicle set alight by arsonists.

Figure 2. Aerial view of the Neerabup fire.

Figure 3. Equipment bogged in the peat.

Figure 4. Dinosaur tanker.

Access for equipment and personnel

Access to the peat is one of the main problems that frontline firefighters face, both from the point of view of subterranean fire in peat, and the boggy nature of wet/moist peat. As peat fires can burn both on the surface and in subterranean, the area alight is not clearly visible. The thin dried surface can easily break with limited pressure, and there are extremely hot areas underneath the surface that are not easily apparent from anywhere other than in wetlands themselves (Santa Barbara County 2000). Thus, while the terrain may appear capable of

supporting the weight of equipment, this is not always the case. An example is provided by the extensive bush fire in February 2001 in Neerabup, north of Perth on the Swan Coastal Plain: this fire spread across an area of around 1500 ha (Fig. 2). The area around Lake Neerabup was severely affected, and as a result, a significant area of peat ignited and burnt for a number of months. Further, where there was wet/moist peat, during the fire, it was recorded that in one area alone up to four fire appliances and two earth moving machines broke through the dry surface of the peat and became bogged in the underlying wet peat (Fig. 3). Fortunately, these areas were not on fire at the time, but if left too long the equipment could have been exposed to the creeping subterranean fire.

One cannot overstate the adverse consequences of having equipment disabled during a bush fire emergency – not only are these resources needed to combat the incident, but they are also potentially in a situation where they could sustain damage. Additionally, personnel could find themselves in a position of suffering injury while retreating from their disabled appliances or while trying to recover them.

Ultimately, of course, in the situations described above, equipment will have to be recovered, and this has implications for the Incident Manager, who has limited resources and may have a very complex bush fire to manage. Firstly, additional resources will have to be found to assist with the recovery operation possibly further depleting the available firefighting equipment resource base, and secondly, personnel will have to be assigned to assist with the recovery operation. The Incident Manager needs to keep the safety of the personnel in the forefront of their mind, whilst continuing to manage a complex bush fire.

Traditional extinguishment methods

As noted above, peat fires are particularly difficult to extinguish. The traditional strategy for extinguishing the peat fire is by saturating the area using large tankers (Fig. 4). Where this cannot be achieved, an alternative has been to isolate the peat area by the installation of a mineral earth fire break commonly installed by using earth moving machinery such as front end loaders. This method would limit the extension of the fire but would not extinguish it, therefore, it should be expected that there will be some smoke in the area from the burning peat, until the peat either burns itself out, or winter rains flood the area and extinguish it.

In a particular case example at a fire in the vicinity of Lake Jandabup in February 2004, the Incident Manager concluded that the isolation of the peat was the only alternative available to prevent a further extension of the fire, since the resources required to saturate the area were not available. Once the peat was isolated, the area was monitored over a period of 6 days, during which time pockets of peat was still burning in close proximity to fire breaks (Fig. 5); these were extinguished using copious amounts of water from the patrolling fire appliances. From an environmental point of view, if the peat fire is not extinguished then there has to be realized that the burning peat will cause smoke pollution for some time well after the initial fire.

Figure 5. Fire burning through peat.

Safety of fire-fighting personnel and the public

Peat fires pose particular safety issues for firefighters. For instance, personal protective equipment at fire scenes is important for personnel, particularly whilst fighting subterranean bush fires. Protective coat, boots and helmet should be mandatory, however, in regard to smoke, or burning subterranean fuel, or hot ashes, eye protection and gloves are equally essential. For instance, in the case of the Brookton/Pingelly bush fire, a firefighter lost all of his fingers on one hand and several from the other as a result of falling into hot ashes.

Areas of demarcation need to be established to restrict access to fire-affected areas, particularly where peat has ignited. This restriction may also have to apply land owners and their families, until the Incident Manager can be sure that there is no risk of people or animals breaking the surface into the subterranean fire. This restriction may have to be in place for days, weeks or even months.

The level of smoke and airborne contaminants that firefighters and neighbours may be exposed to during the firefighting operation also needs to be evaluated. Smoke contains particulate matter, which can irritate the eyes, nose, throat and lungs, and can lodge in the lungs and cause health problems. Smoke can cause particular difficulties for people with existing respiratory or heart problems (see Hinwood & Rodriguez 2005, this issue). While one would expect that firefighters do not have predisposed respiratory conditions, a precondition for FESA recruitment (Fire & Emergency Services Authority 2005), consideration must be given to these smoke pollutants with respect to the wider community.

Global and local health issues

Global

During the 1997–98 forest and land fires in Indonesia and Malaysia, an area of approximately 10 million ha of land was burnt, and although only 15% of this land was in peat areas, the peat fires contributed an estimated 60% of the smoke and haze (Peat-Portal 2002). The ninth ASEAN Ministerial Meeting on Haze in June 2002, for instance, discussed the issues of fire prevention and control in peatlands (Kamal *et al.*, 2003). These meetings were held as a result of the significant haze that affected the southeast Asian region, primarily as consequence of peatland and other vegetation burning. While the Swan Coastal Plains will not have the degree of problems that were experienced during the 1997–1998 fires in Southeast Asia it is still worth considering: (1) how long will the peat burn; (2) the environmental impacts of the fire; (3) the health effects to the public and nearby residents; and (4) the cost and consequences of leaving the fire burn. Thus, the Incident Manager must consider the ultimate social and environmental cost factors, which can vary from lost productivity of the fire and emergency services and on going response calls, to the relocation of residents.

Local

A fire near Lake Carabooda north of Perth provides an example where there was need to relocate residents because of smoke problems. Peat had been burning for a significant time, and eventually feeling that the nearby family's health may be affected, a resident requested atmospheric monitoring be undertaken by the Western Australian Department of Environment Protection Response Unit (WAEPRU). Subsequent monitoring confirmed that the concentrations of contaminates were close to the upper limit of the acceptable levels (pers comm., Peter May of WAEPRU, 26/08/2000). The Local Government was concerned about the health effects to residents and carefully considered a range of options, including the relocating the residents to temporary accommodation.

Conclusions

Fire managers must consider the safety of firefighting personnel, the safety of the local community, and the environmental consequences of their actions when accessing peat fire areas. They also need to be mindful that appliances and equipment can easily break the surface of peat, resulting in the bogging of equipment. The level of access that the public has to fire-grounds must be critically assessed, particularly where peat is involved. This includes the time period after the surface fire has passed, which may be days, weeks or months. If peat is left to burn or smoulder, respective government agencies will have to evaluate the possibility of health and welfare risks posed to the public in the vicinity of smoke and fumes. However, in the overall perspective, prevention of fire is preferable to the need to respond firefighting resources – even the best equipped fire service in the world will need the next significant rains to extinguish extensive peat fires. All fire, land management, government agencies and other interest organisations in Western Australia need to co-operate to develop policies, strategies and tactics that personnel in the front line can use to effectively and efficiently deal with peat fires while concurrently protecting the ecosystems and environment. In the interest of prevention, government agencies, land managers and other interested organizations need to develop strategies that will see the reversal of reduced water levels in wetlands and define pre-planned response mechanisms and capabilities including restrains that have to be considered or followed.

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Preventing wetland soils and sediments from burning on the Swan Coastal Plain: workshop outcomes and conclusions

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Introduction

The workshop sought to review the social and environmental impact of fire on organic-rich soils and sediment and how best to mitigate the risk or reduce the consequences of the fires, in the light of the significant conundrums fire managers face. The objective of the workshop was to collectively consider the relevant scientific and technical information on organic-rich soils and sediments provided by a range of presenters, and then to have the audience participants determine a range of alternative prevention or responses, to protect the soils and minimise their vulnerability to fire. High on the priority list was a recognised need to prevent fires from entering wetland soils or sediments. Further considerations included the needs of both the built and the natural environments.

In convening the workshop, representatives from the Fire and Emergency Services Authority (FESA) and Edith Cowan University (ECU) identified that these issues needed to be addressed by a reasonably broad spectrum of people, including experts in areas associated with organic-rich soils and ecological processes, bush fire managers and community members. The workshop followed invited paper presentations which provided the necessary technical information (the papers published in this issue). The workshop then sought the attendees' participation to prepare some recommendations for more effective consideration of issues raised by fires in these habitats.

Specifically, participants were placed at predetermined seating at tables (seven tables consisting of six persons per table, each person at the table from a different agency or organisation). Each table was then asked to examine a range of scenarios concerning fire and wetlands, and to record their findings. These records are summarised here.

Workshop outcomes

Two principal recommendations were made by workshop participants. The first related to more appropriate management of the superficial aquifers on the Swan Coastal Plain. The second was for more effective and broadly based fire management planning to occur.

1. Management of the superficial aquifers on the Swan Coastal Plain

An issue consistently raised by presenters and workshop participants was the sustainability of the current superficial aquifer management and the way the sites with organic-rich soils and sediments are no longer being seasonally inundated with the winter rains and saturated during drier months. Participants felt unable to make specific recommendations other than 'more appropriate management' involving careful consideration of local drawdown effects resulting from local groundwater abstraction activities where such sites occur, and calling for decision makers to recognise the significant consequences of overall groundwater drawdown for such sites.

2. Fire Management Plans

The principal requirement raised by each working group was for more effective planning to prevent fires from entering organic rich wetland soils or sediments. Fire management plans were seen to be the most useful tool in this regard, and it was consistently argued that the following elements need to be covered in such plans:

A. Mapping of susceptible soils and sediments

B. Community participation

C. Maintenance of moisture levels in wetlands

D. Hazard reduction practices

E. Fire response plans

Other components of the fire management plan would include asset protection (both private property and environmental assets), and people management for smoke contamination, traffic and fire fighter access. People management includes the identification of community stakeholders and utilising their skills and knowledge, and of paramount importance is the safety of the community. In addition the areas of fire management planning where there is an information deficiency will be identified, and where possible, action taken to correct the deficiency.

A. Mapping of susceptible soils and sediments

Improved diagnostic capabilities for sites with vulnerable organic-rich soils and sediments provided in this issue (Semeniuk & Semeniuk 2005, this issue) gives fire managers the capacity to identify critical sites through mapping, an essential precursor for

preparedness, prevention and recovery objectives and strategies. Once the organic-rich sites are identified there is also an opportunity to map and develop strategic access tracks. In addition, to provide access, tracks could compartmentalise the various vegetation areas, for example the delineation and separation of organic sites from surrounding areas.

A component of the fire management plan should also include risk mapping and options to mitigate that risk. This hazard identification must be a genuine appreciation of the total hazards and values at risk. The utilisation of the predetermined protection of life, property and environment plan must be comprehensive enough to ensure the specific values identified are appropriate. There may be a need to prioritise certain areas that leads to some property values being compromised initially to prevent the bush fire entering the high organic soils areas. Once a fire commences in these vulnerable sites it may pose a longer term risk to lives, homes and community values such as smoke free air.

B. Community participation

As community values will be at risk it was considered essential to ensure local engagement in the process of planning. A community awareness and education strategy implemented for all stakeholders was regarded as a key step. A component of that community awareness could include the surveillance and vigilance of critical, identified sites by landowners or neighbours. This vigilance could include early reporting of smoke sightings and also surveillance for suspicious activities that should be passed to Crime Stoppers. The target groups for the community awareness and education must include the general public, local residents, staff from all relevant State and local governments, fire fighters and nature conservation groups. The mediums to be used to ensure that the awareness and education information gets to the appropriate audiences must include local public meetings, local newspapers, posters, radio, television and the internet. Workshop participants highlighted the need for specialised programs for residents and landowners who live adjacent to wetland areas.

C. Maintenance of moisture levels

In some instances, there may be a need to consider artificial water level management of the sites to ensure that the moisture content of the organic-rich soils does not drop to a level that will sustain ignition. This may include the albeit very expensive option of flooding critically important sites, or sites where risk to other values is particularly high, to sustain them over periods of drought or periods during which they are vulnerable to burning.

D. Hazard Reduction

The fire management plan may also need to have a hazard reduction plan developed so that inappropriate hazard reduction work is not undertaken. If an option such as prescribed burning is deemed to be inappropriate at that specific site, then the fire management plan needs to ensure that the reasons why the hazard reduction method is not appropriate are recorded. Simultaneously

it should also record what the boundaries are of the restrictions on those activities. Alternatively if a hazard reduction method is preferred then that option also needs to be clearly described along with reasons why that option was chosen and specifying the appropriate constraints on its application. For example if slashing is considered an appropriate activity in the bush land adjacent to wetlands, plans need to be prescriptive: how to slash, the extent and relative distances from the sites to be protected, and how to manage the dead and down vegetation.

E. Fire Response Plans

Fire response plans are important as they provide a pre-determined tool to ensure that fire fighters are able to respond appropriately to meet the fire, and the social and environmental needs of sites. Given the special nature and specific needs of these sites it is important to ensure values are not compromised through a lack of communication. Some of the response measures that should be considered for appropriateness include:

- fire breaks,
- the use of fire suppressants,
- the application of trenching machines and/or
- the strategic placement of bores to prepare for flooding.

Preferred options should be done in the light of a full consideration of the benefits and costs, both financial and environmental needs. Included in this analysis must be the costs of mitigating the environmental damage that may result as a consequence of suppressing the fire (for instance the water quality implications; Horwitz & Sommer 2005, this issue) and also the consequences of leaving a fire to burn until conditions other than human intervention (i.e., rainfall or elevation of groundwater levels) resulted in its suppression.

A consideration of the fire response plan must be whether the community and environmental values would be better protected by allowing the site to be burnt until nature provides rainfall and raises the soil moisture content. The vexed nature of this question: whether to actively suppress the fire or not, whether to use suppressants or not, whether to trench or not, will inevitably result in some people feeling disenfranchised by decision making, again stressing the importance of involving stakeholders in planning processes.

Some further considerations for fire managers

The development of fire management plans and fire response plans should improve the potential to protect the community and the environmental values. While it is desirable to have these plans developed in the short term, the need for additional information that will become available through research recognised as important by workshop participants may result in the development of some plans being delayed.

During the workshop it was consistently identified that community participation and communication is essential. FESA currently operates a system of urban bushland fire response plans, that have community participation. It may be possible to expand that system to cover sites with organic-rich soils and sediments.

It is important that the community recognises that FESA will be undertaking bush fire suppression work with the best will to minimise environmental, social and community damage. In many bush fires there will be some potential damage to each component. It should also be acknowledged that bush fires are suppressed by people using their judgement and skills in difficult conditions, against an unpredictable natural event, bush fires. People who review the performance of fire managers must consider the events as a whole and not in individual components, as there will be positives and negatives in each component.

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Native insect flower visitor diversity and feral honeybees on jarrah (*Eucalyptus marginata*) in Kings Park, an urban bushland remnant

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Abstract

This study aims to determine firstly the diversity of native insect visitors to flowers on the mass-flowering canopy tree jarrah (*Eucalyptus marginata*), and secondly the relative abundance of feral honeybees and native insects visiting jarrah flowers. Flower density and nectar production were measured, and observations of animals visiting flowers were made during peak flowering of jarrah in Kings Park. Insects were the most commonly observed floral visitor; 83 species from 63 genera in 38 families across 5 orders were recorded. The overall richness and abundance of insect species visiting jarrah flowers changed through the day. Feral honey bees were by far the most common visitor, accounting for 47 % of observations, and suggesting they are a significant pollinator of jarrah in Kings Park. However, the presence of a number of exclusively nectar- and pollen-feeding native bees and flies, and native anthophilous tiphid wasps and beetles, suggests that the native fauna is still effecting some pollination. The diversity of insects observed visiting jarrah flowers is higher than reported for other eucalypts throughout Australia, and confirms that remnants like Kings Park are significant for the conservation of biodiversity.

Keywords: native insects, feral honeybees, *Eucalyptus marginata*, jarrah flower visitors

Introduction

Remnants of native vegetation in Australian cities are important community assets that form parts of regional conservation networks and provide unique opportunities for recreation and conservation education. However, in many urban bushland reserves the impacts of fragmentation and changed disturbance regimes are transforming community structure and species composition with some species declining in abundance, some species showing no change and others (predominantly exotic species, though not always) increasing in abundance (Kirkpatrick 1988; Recher & Serventy 1991; Dixon *et al.* 1995). Understanding the impacts of changes in species composition on functional interactions such as pollination is vital for organisations vested with the management of urban bushland. In particular, the management of exotic species may be problematic. For example, removal of exotic species may have a net positive effect for native species, no net effect, or a net negative effect if the exotic species is fulfilling a functional role that has been lost. The ecological consequences of removing exotics, therefore, needs to be assessed before implementing a control program. For example, feral honey bees are widespread in Western Australia's urban Kings Park bushland and Dixon *et al.* (1995) recommend the removal of colonies. However,

little is known about the relative abundances of honey bees and native insect pollinators in the bushland. A recent study in Argentine subtropical dry forest observed that the frequency and taxon richness of native flower visitors on mass flowering trees declined with decreasing forest fragment size but frequency of visits by feral honey bees increased in a complementary fashion (Aizen & Feinsinger 1994). It is therefore possible that feral honey bees are now the major insect pollinator in Kings Park bushland and their removal could have a negative effect on seed production in plants which have generalist insect pollinators.

This study aims to determine firstly the diversity of native insect flower visitors on the mass-flowering canopy tree jarrah (*Eucalyptus marginata*) in Kings Park, and secondly the relative abundance of feral honeybees and native animals visiting jarrah flowers. Establishing the diversity and relative abundance of native insect flower visitors will provide vital information for decisions concerning the potential removal of feral honeybee colonies in Kings Park.

Methods

Study Site

The Kings Park bushland is a 267 ha remnant of mixed *Eucalyptus-Banksia-Allocasuarina* woodland located approximately 1 km from the Perth Central Business

District. Jarrah is a dominant canopy species in the woodland. Kings Park is isolated from other native vegetation by urban development to the north and west, and by the Swan River to the south and east. The bushland is highly disturbed and of the 578 plant species recorded, 246 are native, 217 are naturalized aliens, 30 are naturalized and native to other parts of Western Australia and Australia, and 80 are planted but not naturalized (Barrett & Tay 2005). Despite this, the Kings Park bushland has significant conservation values and is an important component of the nature reserve system on the Swan Coastal Plain (Anon. 1981). More recently a planning guide outlining objectives and recommendations for the conservation management in the bushland has been published (Dixon et al. 1995). Kings Park bushland is isolated from other native vegetation by urban development to the north and west and by the Swan River to the south and east. Perth has a warm Mediterranean climate characterised by hot dry summers and mild wet winters. The mean monthly maximum air temperature ranges from 31° C in February to 18°C in July; mean annual rainfall is 774 mm of which 80% falls in the winter months between May and September (Bureau of Meteorology 2005).

Jarrah (*Eucalyptus marginata*)

Jarrah is an endemic tree or mallee of southwestern Australia (Abbott & Loneragan 1986) and is the most important hardwood in Western Australia. Jarrah most commonly grows as a tree and is a dominant in forests and woodlands. There has been considerable research on the ecology and silviculture of jarrah (Abbott & Loneragan 1986; Dell et al. 1989; Stoneman & Dell 1994; Stoneman et al. 1994), but little is known about its reproductive biology and pollination ecology. Information on pollination is limited to mainly opportunistic observations (Brown et al. 1997). Currently there are 15 records of ten animal species visiting jarrah flowers; these are four birds (western spinebill, brown honeyeater, new holland honeyeater, purple-crowned lorikeet), one mammal (honey possum), three jewel beetles, an evaniid wasp and a therevid fly (Brown et al. 1997).

Jarrah produces bud primordia annually in the axils of new leaves from late summer to early autumn (February – April) (Abbott & Loneragan 1986; Davison & Tay 1989). In many years the new buds are aborted during the winter and spring but in some years they continue to develop and flower in late spring and early summer (September – January) (Abbott & Loneragan 1986; Davison & Tay 1989). Little is known about the factors which favour the retention of buds but flowering has been described as occurring every 4 – 6 years by Abbott & Loneragan (1986) and every 2 – 3 years by Davison & Tay (1989).

Jarrah inflorescences are unbranched, have 7–21 flowers each 15–20 mm in diameter which are borne in the leaf axils near the outside of the canopy. Individual white stamens up to 8 mm long are splayed upwards and outwards from the rim of the hypanthium forming a flat-topped array 15–20 mm in diameter, and exposing a nectar-producing disc. The ovary roof lies about 2 mm below the hypanthium rim; the style is short (8 mm) and emergent with the stigmatic tip projecting 2 mm above

Table 1

Characteristics of the trees used in the study.

Tree	Height (m)	DBH (cm)*	Canopy width (m x m) **
1	8.5	28	8 x 6
2	14.5	50	12 x 9
3	7.2	18, 17	5 x 4
4	14.4	59	12 x 11
5	5.3	8, 8, 8, 10, 5, 6	3 x 3
6	11.2	26	6 x 5
7	18.8	48, 59, 51	18 x 15

* Trees with more than one DBH are multistemmed; ** Canopy width measurements were made at the widest axis and perpendicular to the widest axis

the level of the tops of the stamens when the flower is fully open. Like all other eucalypts jarrah is protandrous with anthers dehiscing before the stigma becomes receptive. As a consequence adjacent flowers within and between inflorescences can be in the male or female phase (House 1997).

The trees used in the study were centrally located within the 270 ha bushland remnant. The trees ranged in height from 5.3 m to 18.8 m and in canopy width from 3 m x 3 m to 18 m x 15 m (Table 1). Flower density (number of flowers in 1 m³ of foliage) was estimated at two points in the lower canopy of five trees.

Nectar measurements were made on flowers from three trees. In each tree at two positions in the lower canopy a cluster of mature flower buds was enclosed with a 1 mm mesh bag to exclude flower visitors. The progress of buds towards flowering was checked daily and approximately 72 hours after anthesis, bagged clusters of flowers were harvested and nectar measured with 2 ml micropipettes on 10 fully opened flowers. The volume of nectar collected from each was often very small and concentrated, and consequently samples for individual trees were combined, and then diluted with 20 ml of de-ionised water for measurement of % sucrose concentration (w/w) with a temperature compensated 0–50% Bellingham & Stanley pocket refractometer. The original concentrations of the nectar samples were calculated from the diluted concentrations with the formula (wt of nectar + wt of water/wt of nectar) x sucrose concentration.

Observations of flower visitors

Detailed observations of flower visitors were made on seven trees over seven days during peak flowering in mid November in 1997. Observations were made on three trees per day, and were restricted to branches up to 5 m from the ground. In each tree at three locations, 2 m³ of canopy was measured with a tape and marked, and the richness and abundance of animals visiting flowers counted for two independent 5 minute intervals (30 minutes total for whole tree). During the first three days of the survey censuses were made at three times of the day: morning (06:00–08:00 hrs), midday (11:00 –13:00 hrs) and evening (16:00–18:00 hrs). After three days it became evident that animal activity at flowers was greatest at midday (11:00–13:00 hrs), and subsequent observations were restricted to that period. Sunrise and sunset for the study period were 05:11–05:06 hrs and 18:49–18:58 hrs

respectively. Insects were identified as morpho-species in the field with voucher specimens of each taxon determined at least to family by Dr T Housten and Mr B Hanich (Department of Terrestrial Invertebrates, Museum of Western Australia).

Statistical analyses

Analysis of variance was used to compare the abundance and richness of insects according to the time of day and insect species for the three most common orders: Hymenoptera, Coleoptera and Diptera. Values were transformed prior to analysis using the square root transformation to stabilise variance. The combination of tree and day of measurement was used as a random effect while the time of day and insect species were fixed effects. A Kruskal-Wallis test was used to compare the proportion of bees (total of feral and native honeybees) that were native bees over the three sampling times; morning, midday and afternoon. Values are given as mean ± standard error (sample size).

Results

Flower Density and nectar measurements

The mean flower density was 1334 ± 165 (n=10) flowers m^{-3} of canopy. The mean volume of nectar per flower was 0.64 ± 0.22 ml (n=30), and the mean sucrose concentration of nectar was 55.27 ± 7.81 % (n=30).

Observations of flower visitors

The 3278 observations of insects visiting jarrah flowers found 83 species from 63 genera in 38 families across 5 orders. A list of all insects observed visiting flowers is given in Table 2. Only three observations of birds visiting jarrah flowers were made; these were one red wattlebird (*Anthochaera carunculata*) and two brown honeyeaters (*Lichmera indistincta*). Feral honeybees (*Apis mellifera*) were by far the most common floral visitor accounting for 47% of insect observations (Fig 1). Beetles were seen in 18.6% of observations followed by flies (12.0%), ants (8.8%), native bees (6.4%), wasps (5.5%) and moths and butterflies (1.7%).
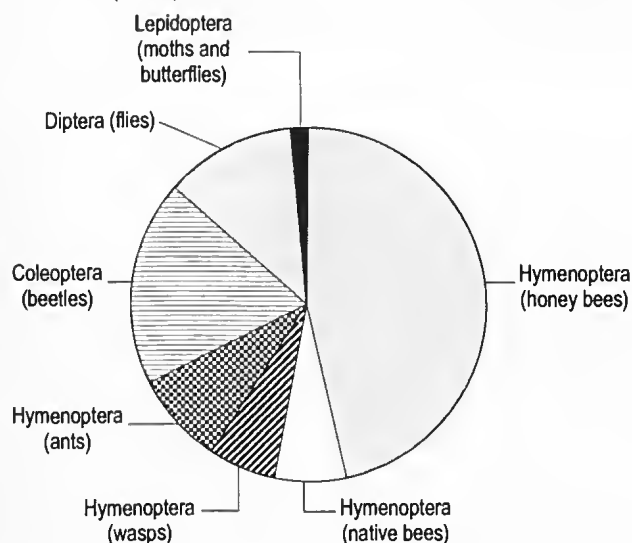
Figure 1. The proportion of all floral visits accounted for by the most abundant insect orders; Hymenoptera, Coleoptera, Diptera and Lepidoptera.
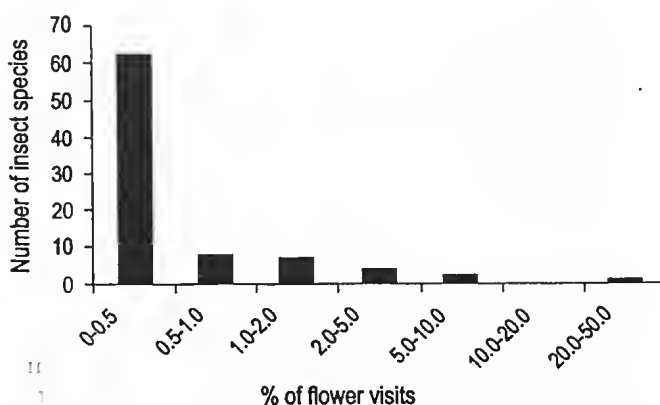
Figure 2. The number of insect species in classes defined by the percentage of floral visits.

The distribution of insect species in classes defined by the number of floral visits is strongly right skewed; 62 species were recorded on fewer than 0.5% of occasions, 8 species on 0.5–1.0% of occasions, 7 species on 1.0–2.0 % of occasions, 4 species on 2.0–5.0 % of occasions, 2 species on 5.0–10.0 % of occasions and 1 species on more than 20% of occasions (Fig 2).
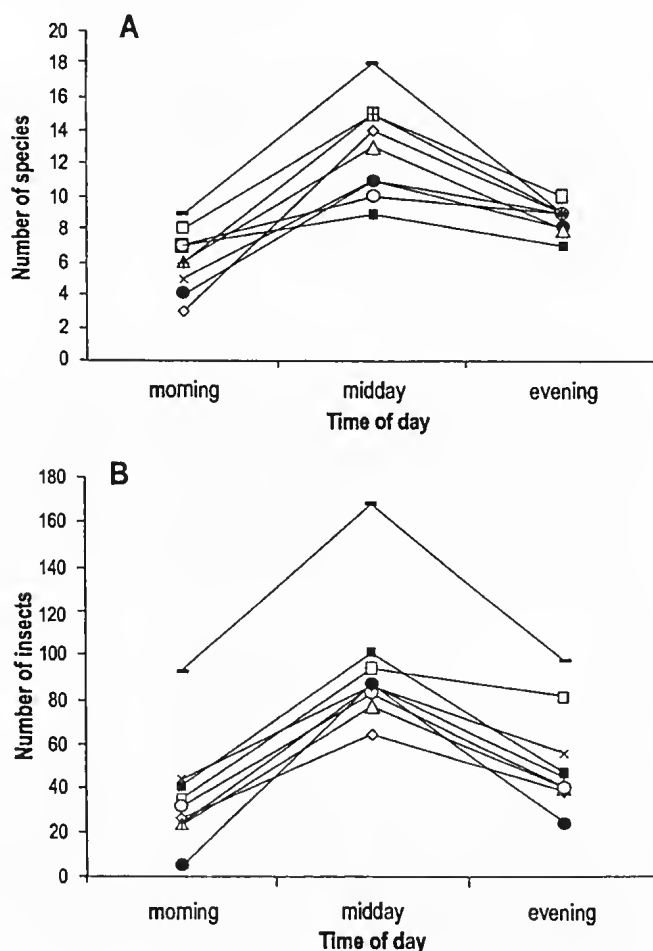
Figure 3. Diurnal data plots showing maximum insect activity at midday in terms of (a) the number of species, and (b) the abundance of insects visiting jarrah flowers. Data are presented for three times of the day; morning (0600–0800 hrs); midday (1100–1300 hrs); and evening (1600–1800 hrs). Observations were made on three trees on each of three days; each symbol represents one tree.

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Table 2

Insects observed visiting *Eucalyptus marginata* flowers.

Blattodea	Coleoptera	Diptera	Hymenoptera	Lepidoptera	Neroptera
Blattellidae	Buprestidae	Bibionidae	Apidae	Lepidoptera gen sp	Mantispidae
Ellipsidion sp	*Castiarina rufipennis*	*Bibio imitator*	*Apis mellifera*	Lycaenidae	Mantispidae gen sp
Ellipsidion sp	Carabidae	Bombyliidae	*Exoneura sp*	*Nacaduba biocellata*	
	Scopodes sp	*Composia tendens*	*Thyreus waroonensis*	Nymphalidae	
	Cleridae	Calliphoridae	Bethylidae	*Geitoneura klugii*	
	Eleale aulicodes	*Calliphora sp*	Bethylidae gen sp	*Vanessa kershawi*	
	Eleale reichei	Calliphoridae gen sp	Braconidae		
	Eleale sp	Chloropidae	Braconidae gen sp		
	Lemidia sp	Chloropidae gen sp	Colletidae		
	Phlogistomorpha sp	Chloropidae gen sp	*Euryglossina (Euryglossina) perpusilla*		
	Zenithicola sp	Conopidae	*Hylaeus (Euprosopis) violaceus*		
	Coccinellidae	Conopidae gen sp	*Hylaeus (Prosopisteron) quadratus*		
	Coccinella transversalis	Muscidae	*Hylaeus (Prosopisteron)* sp nov. A28		
	Menochilus quadriplagiatus	Muscidae gen sp	*Hylaeus (Prosopisteron)* sp nov. A216		
	Curculonidae	Muscidae gen sp	*Hylaeus (Rhodohylaeus) proximus*		
	Meriphus sp	Muscidae gen sp	*Hylaeus (Rhodohylaeus) rufipes*		
	Dermestidae	*Musca vetustissima*	*Leioproctus (Leioproctus) sp*		
	Anthrenocerus sp	Mycetophilidae	*Pachyprosopsis (Pachyprosopula) purnongensis*		
	Neoanthrenus sp	Mycetophilidae gen sp	Evaniidae		
	Trogoderma sp	Nemestrinidae	Evaniidae gen sp		
	Mordellidae	*Trichopthalma sp*	Formicidae		
	Austromordella sp	Sarcophagidae	*Camponotus sp*		
	Mordellistena sp	Sarcophagidae gen sp	*Dolichoderus sp*		
	Rhipiphoridae	Sepsidae	*Iridomyrmex sp*		
	Evaniocera sp	Sepsidae gen sp	*Myrmecia sp*		
	Scarabaeidae	Syrphidae	*Polyrachis sp*		
	Automolius sp	Syrphidae gen sp	Formicidae gen sp		
	Tenebrionidae	*Xanthogramma sp*	Formicidae gen sp		
	Chromomoea sp	Therevidae	Gasteruptiidae		
		Therevidae gen sp	*Gasteruption sp*		
			Gasteruption sp		
			Gasteruption sp		
			Halictidae		
			Homalictus dotatus		
			Lasioglossum (Chilalictus) castor		
			Lasioglossum (Chilalictus) sp		
			Lasioglossum (Parapsecodes) sp		
			Noma flavoviridis complex		
			Ichneumonidae		
			Ichneumonidae gen sp		
			Megachilidae		
			Chalicodoma (Hackeriapsis) sp		
			Chalicodoma (Hackeriapsis) sp		
			Megachile (Mitchellapis) fabricator		
			Pompilidae		
			Pompilidae gen sp		
			Tiphiidae		
			Tiphiidae gen sp1		
			Tiphiidae gen sp 2		
			Tiphiidae gen sp 3		

Diurnal patterns of flower visitors

The number of species and abundance of insects visiting jarrah flowers changed through the day and was lowest in the morning (06:00–08:00 hrs), and highest in the middle of the day (11:00 – 13:00 hrs). This trend was consistently observed on all trees on all days (Fig 3). However, changes in the number of species and number of insects visiting flowers through the day were different across the three most abundant insect orders, with the interaction between the time of day and insect order being highly significant ($F = 3.60$, d.f = 4, $P = 0.014$ for number of species, $F = 4.37$, d.f. = 4, $P = 0.006$ for number of insects). Hymenoptera species number and abundance were significantly lower in the morning and significantly higher at midday compared to the evening; Coleoptera species number and abundance were significantly higher at midday than in the evening or in the morning; Diptera species number and abundance did not change significantly through the day (Fig 4).

The relative proportion of native bees to feral honeybees changed significantly through the day ($H = 9.59$, d.f. = 2, $P = 0.009$) due to the fact that no native bees were observed during the mornings. Overall, the proportions of insects of the different orders observed at different times of the day were as follows. In the morning feral honeybees accounted for 45.7% of observations, flies (23.3%), ants (18.9%) and beetles (12.2%); in contrast native bees, wasps, moths and butterflies were never observed during the morning. In the middle of the day

feral honeybees accounted for 49.3% of observations, beetles (20%), ants (11.7%), flies (10%), native bees (4%), wasps (3.2%) and moths and butterflies (1.8%). In the evening feral honeybees accounted for 41% of observations, flies (23.5%), ants (25.3%), beetles (7.6%), native bees (2%) and wasps (0.6%).

Discussion

Jarrah is a generalist mass-flowering eucalypt and it attracts a diverse array of floral visitors including birds, mammals and insects. Prior to this study there were only 15 records by ten animal species visiting jarrah flowers; these were western spinebill, brown honeyeater, new holland honeyeater, purple-crowned lorikeet, honey possum, three jewel beetles, an evaniid wasp and a therevid fly (Brown *et al*. 1997). The results of this study substantially expand the list of insect visitors, with insects being the most commonly observed group.

The low number of vertebrates observed visiting jarrah flowers may be attributable to a number of site-specific factors and the proximity of the observer to flowers. Firstly, vertebrate visitors such as purple-crowned lorikeets (*Glossopsitta porphyrocephala*) and honey possums (*Tarsipes rostratus*) are locally extinct in Kings Park (Recher & Serventy 1991; Dixon *et al*. 1995). Secondly, during the study there were abundant alternative nectar resources which may not always be available when jarrah is flowering. In 1996 a fire burnt 30% of the Kings Park bushland, and as a consequence the post-fire opportunist *Anigozanthos manglesii* was flowering. In addition, the grass tree *Xanthorrhoea preissii* was flowering across the entire bushland which is evidently a rare event (Baird 1977). Honeyeaters were observed on both species. It is possible that in years when this concurrent flowering does not occur, birds may be more commonly observed on jarrah flowers. Finally, the close proximity of the observer to flowers whilst not affecting insect visitation rates may have displaced birds.

Despite the potential influences of site and methods, jarrah's floral nectar characteristics provide further evidence that the species is commonly insect-pollinated. The concentration and volume of nectar affect the type of animals foraging on flowers (Proctor *et al*. 1996). Insect-pollinated flowers typically produce relatively lower volumes of nectar with high concentrations of sugar (>50%). In contrast, bird-pollinated flowers produce relatively larger volumes of nectar with low concentrations of sugar (15–25%). The volume of nectar produced by jarrah flowers (0.64 ml) is considerably less than that reported for the large red-flowered bird-pollinated species *E. macrocarpa* (82.0 ml: Collins & Briffa 1982; *E. rhodantha* (mean ± SE = 21.21 ± 39.54 ul; McNee 1995, and *E. caesia* subsp *caesia* (109.6 ± 34.3 ul) and *E. caesia* subsp *magna* (298.4 ± 103.2 ul) (Hopper & Wyatt, unpublished observations). Furthermore, nectar concentration of jarrah flowers (55.3%) was higher than that reported for large red-flowered bird-pollinated species, *E. macrocarpa* (12%, Collins & Briffa 1982), *E. rhodantha* (22–37%, McNee 1995), and *E. caesia* subsp *caesia* (12–24%), and *E. caesia* subsp. *magna* (12%) (Hopper & Wyatt unpublished observations). Considerable caution needs to be applied to the above interpretation as nectar volumes and concentrations
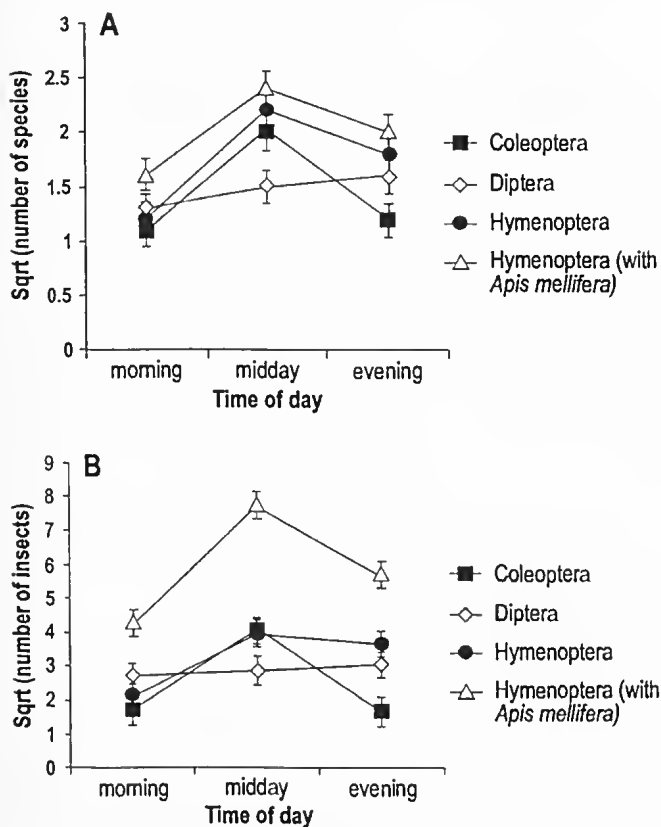

Figure 4. The (a) mean number of insect species, and (b) mean abundance of insects visiting jarrah flowers in each of the three most abundant orders Coleoptera, Diptera and Hymenoptera for three times of the day; morning (0600–0800 hrs); midday (1100–1300 hrs); and evening (1600–1800 hrs). Data were square root transformed to stabilise variances. Error bars are ± S.E.

measured in this study maybe lower and higher respectively than those normally encountered by the animals (the nectar initially secreted in bagged flowers had up to 3 days for water to evaporate). Nevertheless the floral reward offered by jarrah flowers is considerably less than that recorded for red-flowered bird-pollinated species. A similar pattern was evident in the nectar production data recorded by Paton & Ford (1977) for the small-flowered generalist *E. gracilis* compared with the larger-flowered *E. cosmophylla* and *E. leucoxylon*.

The diverse array of insects observed visiting jarrah flowers (83 species from 65 genera in 39 families) is considerably higher than that reported by a very limited number of other studies. Ireland & Griffin (1988) observed 41 insect species from 29 families in 4 orders visiting *E. muelleriana* flowers in open forest in Victoria, and Hawkeswood (1989) observed 11 insect species in 5 genera from 4 families in 2 orders on *E. foecunda* and *E. cylindrifolia* flowers in mallee woodland in Western Australia. The number of insect species observed on jarrah flowers is also higher than that reported for related shrub and tree species in the family Myrtaceae. Hawkeswood (1981) observed 13 species of insect from 12 genera in 4 families visiting the tree *Angophora woodsiana* flowers in open forest in Queensland. O'Brien & Calder (1993) recorded 23 genera in 15 families from three orders visiting flowers on the shrubs *Leptospermum myrsinoides* and *L. continentale* in coastal heath and open woodland in Victoria. It is highly likely that the number of insect flower visitors to jarrah over its widespread distribution exceeds that recorded in Kings Park.

Most of the 39 insect families observed visiting jarrah flowers have been described as visiting flowers in other eucalypt species (Ashton 1975; Bond & Brown 1979; Hawkeswood 1981; Ireland & Griffin 1988; House 1997), or in other Myrtaceae (Hopper 1980, Hawkeswood 1981b; O'Brien & Calder 1993), or other Australian plant taxa (Armstrong 1979). Most of the insects visiting jarrah flowers are potential pollinators, with the exception of two families Carabidae (Coleoptera) and Mantispidae (Neuroptera) which are predominantly predacious and were therefore unlikely to be exploiting floral resources. This is because, firstly, the small open cup-shaped jarrah flower has no petals but presents a ring of stamens that act as a support for nectar and pollen feeding insects. As a consequence, most insects visiting the flower must come into contact with anthers and probably stigmas. Secondly, all eucalypts studied to date are protandrous and have a mixed mating system that combines outcrossing and inbreeding in varied proportions. Allozyme-based estimates of the rate of outcrossing (t; 0 = complete selfing, 1 = complete outcrossing) range from 0.44 to 0.96 (Potts & Wiltshire 1997). To date no self-incompatible species have been found, and as a consequence insects need only move the relatively short distance between flowers which are in the male phase to flowers which are in the female phase within the same inflorescence to effect pollination (House 1997).

Although the number of insect species observed visiting jarrah flowers in Kings Park was high, many species were recorded infrequently, and honeybees accounted for nearly 50% of observations. Honeybees

have been recorded foraging on flowers of a number of other *Eucalyptus* species (Ashton 1975, Bond & Brown 1979, Ireland & Griffin 1984, McNee 1995, Paton 1996) and over 200 other Australian plant genera (Paton 1996). Generally, knowledge of the use of floral resources by vertebrates far exceeds our knowledge for invertebrates and as a consequence there are few studies describing the diversity of insects sharing a floral resource with honeybees (Hawkeswood 1981a,b; Bernhardt *et al.* 1984; Ireland & Griffin 1984; Kenrick *et al.* 1987; Ettershank & Ettershank 1993; O'Brien & Calder 1993; Paton 1996). As in the present study, where counts and collections of insects on flowers have been made elsewhere, it has been found that honeybees account for half or more of all flower visits (Paton 1996). In Kings Park it is likely that most of the honey bees belong to feral colonies that occur in the bushland (Dixon *et al.* 1995).

There are no published studies of the proportion of floral resources consumed by native insects and honeybees but Paton (1996) concluded that the potential for competitive interactions is considerable and that the proportion of resources consumed by honeybees is similar to or higher than the proportion of visits honeybees make to flowers. Paton (1996) argued that, firstly, in temperate locations honeybees begin foraging one to two hours earlier than native insects and therefore have more or less exclusive use of the flowers at times when nectar and pollen availability are highest; and secondly, as honeybees are larger than most of the native insects visiting flowers they usually remove more nectar or pollen during each visit.

The results of this study show that honey bees are sharing the floral resource with a similar number of native insects at all times of the day; the proportion of flower visits by feral honey bees and native insects was similar regardless of the sampling time. However, the species composition of native insect flower visitors was not constant through the day; native bees, wasps, moths and butterflies were not observed during the early morning but were observed at midday. Clearly, feral honey bees are utilising nectar and pollen resources earlier in the day than these groups of native insect species but not others (ants, beetles and flies). Of course the impact of feral honeybees on native insect floral visitors will depend on the availability of floral resources. If floral resources are not limiting then honeybees will have no impact on native insect flower visitors. Unfortunately, little is known about the temporal availability of floral resources in Kings Park and this is an important area for further study.

Finally, decisions about removal of feral honeybee colonies require an understanding of the role of honeybees as pollinators, and nectar and pollen consumers for species across the entire community. Honeybees may or may not play a role in pollination when frequently visiting flowers. Critical experiments are needed to resolve their role as pollinators (Paton 1996). Jarrah has simple cup shaped flowers open to many potential pollinators. More complex flowers in the Kings Park bushland such as those of native orchids and peas may be affected by honeybees in quite different ways to jarrah. Community level studies are therefore an area for further research.

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Selective feeding by macropods on vegetation regenerating following fire

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Abstract

The role of selective herbivory on plant mortality and density was investigated in naturally regenerating post-fire *Banksia* woodland at Whiteman Park Reserve, Western Australia. The western grey kangaroo (*Macropus fuliginosus*, Desmarest 1817) and black-gloved wallaby (*M. irma*, Jourdan 1837) are the largest native herbivores at the Reserve, and their impact upon the density of selected regenerating plant species in relation to time since fire was assessed. Both exotic and native plant species were well represented in the macropod diet. Density of plants within each species had no effect on selection. Defensive traits such as spinescence and tannin content also had no discernable effect on selection. The effect of herbivory and time since fire upon density was dependent upon plant species, with some species occurring at greater densities in exposed than protected areas. As expected, fire ephemerals declined in density with time, in particular *Austrostipa*, independent of level of herbivory. While herbivory appears to have a greater influence upon species density than fire, outcomes were highly species dependent. Results suggest kangaroos may assist in controlling introduced herbaceous species without detriment to native vegetation so long as populations did not exceed carrying capacities for the Park. The importance of continual monitoring of kangaroo populations is highlighted here, ensuring controlled build-up of combustible plant growth as well as maintaining kangaroo populations at a suitable carrying capacity for the environment.

Keywords: selective herbivory, macropod, post-fire regeneration, plant density.

Introduction

Seedlings and regenerating resprouters determine post-fire species composition in many Australian ecosystems (Leigh & Holgate 1979), with mortality during this vulnerable stage an important factor regulating the pattern of recovery (Harper 1977; Fenner *et al.* 1999). Herbivory may be a highly significant constraint on seedling recruitment (Crawley 1983; Hanley 1998). Selective predation of preferred seedling species has significant consequences for plant community development exerting a profound effect on community species composition (Hanley 1998), as well as on its structural components such as species density (Leigh & Holgate 1979). Substantial evidence indicates a decline in the populations of many plant species over time through selective elimination of their seedlings by herbivores (Lange & Graham 1983; Heinen & Currey 2000; Swihart & Bryant 2001).

For palatable plant species, browsing by native animals after fire may have a more profound effect on plant survival than the fire itself (Leigh & Holgate 1979). At Whiteman Park Reserve, Western Australia, preliminary fencing studies showed foliage cover of native species to be significantly greater after four years of kangaroo exclusion, implying possible adverse effects of kangaroos on native vegetation (Mattiske Consulting 2000). While declines in species abundance and cover are

evident, however, it is important that species composition be also considered. Cover of the weed *Ehrharta calycina*, a major component of the kangaroo diet, was greater in kangaroo exclusion sites. The unpalatable weed *Ursinia anthemoides* was greatest in grazed sites, however, suggesting that feeding habits of kangaroos may favour some species to the detriment of others (Mattiske Consulting 2000).

Mattiske Consulting (1995) suggested that while large kangaroo populations may impact on native vegetation, their feeding activity may be beneficial in terms of fire control if they reduce the weed biomass. An understanding and management of factors affecting seedling survival and recruitment is therefore crucial for correct management of regenerating ecosystems. In 2001, Whiteman Park accommodated 900 western grey kangaroos with a breeding rate of 40 % per year. This breeding rate, facilitated by the presence of water and increased farmland area in the region, has led to a population size far exceeding pre-European estimates. These large numbers of kangaroos led to the implementation of a culling control program in 1991 under a Damage Control License, as it was thought that kangaroo herbivory was adversely affecting the native vegetation. While Mattiske Consulting (2000) reported that western grey herbivory had minimal impact on vegetation four years after plot exclusion, it was evident that kangaroos may reduce the cover of selected native plant species.

The range of plant species subject to damage from

large native herbivores in south-western Australia is extensive. Palatable species show highly variable characteristics. At Whiteman Park, the two primary native herbivores are the western grey kangaroo (*Macropus fuliginosus*) and black-gloved wallaby (*M. irma*). To quantify the impact of these herbivores upon recovering vegetation, native species of high conservation value and introduced species, were monitored following fire in order to test the following hypotheses:

1. the densities of plants in areas protected from macropods should be greater than those of plants exposed in both the short (4 weeks) and long (2 years) term.

2. plant damage is positively correlated with the presence of macropods in the environment.

3. the response of plant species to macropod herbivory varies with differing morphological attributes.

Materials and Methods

Study site

Whiteman Park is situated 20 km north-east of Perth and consists of 3 600 ha of natural bushland and pasture. The vegetation is low woodland dominated by *Banksia attenuata*, *B. menziesii* and *Eucalyptus todtiana* on the upper slots, and *Melaleuca preissiana* and *B. littoralis* in the depressions. On 14 February 2001, a large fire affected much of the conservation area at Whiteman Park. Three sites within this burnt area were chosen to undertake the study. These were chosen to include varied plant communities, topography and soil types (two lowland sites and one elevated coastal dune site), in locations known to be frequented by macropods. These sites were not subjected to any adverse influence of fire fighting techniques (i.e. compaction, vehicle disturbance) to ensure a natural post-fire condition was maintained. Immediately following the fire, fencing was constructed around all study sites to omit all vertebrate access. Invertebrates could not be controlled via fencing, although daily monitoring of regenerating vegetation showed little herbivore activity from this group.

Species survey

A complete species list of naturally regenerating plant species observed growing at three sites of varying topography and soil type (two lowland sites and one elevated coastal dune site) at Whiteman Park was compiled from September to October 2001 (Appendix 2). This was the time of maximal species diversity of annuals. Most plants were identified to species level. Authorities for names follow Paczkowsaka & Chapman (2000). It was not possible to take specimens of the genera *Aira* or *Hypochaeris* to species level due to difficulties identifying individuals. Intermediates of both groups are common, hence it is possible individuals may belong to one of four or two species respectively, or hybrids of members of these species (Hussy *et al.* 1997). For all species encountered, signs of vertebrate herbivory were noted and numbers of eaten and uneaten plants recorded.

Mortality and density: short and long term effects of herbivory

Study areas at the three recently-burnt sites were divided into 10 plots (5 x 5 m) and sectioned into four quarters, using compass bearings to orient the divisions. From the complete species list for each site, ten abundant species of differing morphologies were selected at each site for use in quantification of herbivore effects on plant survival. Study species differed between sites. Densities were calculated using the plotless density method, as described by Mueller-Dombois & Ellenberg (1974). Each individual of the selected species wasto be monitored and marked by a balsa wood pop stick with identification number. These were pushed into the soil, with 2 cm protruding to limit potential interference with herbivore feeding. In plots where plants were not found in designated quarters, densities for these plants were recorded as 200 cm, the maximum distance from the quadrat centre (see Mueller-Dombois & Ellenberg (1974) for density calculation details).

Exclosure fences were modified to expose five of the ten plots at each site to herbivores seven months following the fire, with the time of exposure selected in mid-spring to encompass the presence of annual and geophyte species in the study. Plots were inspected after 4 weeks, and alive/dead status of study individuals and plant densities were recorded again. This allowed assessment of macropod selection patterns, with feeding activity observed consistently over the period, while ensuring annual and ephemeral species had not died down due to natural causes. Weekly spoor assessment was completed, with scats identified and counted in each quadrat. Traces of other species participating in the trials (i.e. rabbits, bandicoot) were not evident throughout the monitoring period. Infrared video filming of site 1 over a four week period following fence amendment supported this assumption, with no other vertebrate herbivore species observed.

Plant species densities were again calculated in October 2003, two years following the first assessment and two and a half years following the fire. Values for exposed sites were compared with densities of those protected in plots of adjacent exclosures (separated by 50 m) that had been fenced from herbivores since the fire. A comparison of plant density for each species with time (2001 and 2003) and position (protected and exposed) was made.

Plant morphology

Two leaves were collected from each of ten plants of each species, and leaf mass:area, leaf thickness and dry density were determined as described by Witkowski & Lamont (1991). Amendment was made to the formula for leaf:mass area and density of needle leaved species, by dividing the standard formula by 0.7854. Leaf area was measured using the Dias system (Delta-T Devices, Cambridge, England). Other characteristics recorded included plant height and moisture content, and chemical attributes as described below. Attributes are provided in Table 1.

Chemical analysis

Whole plant samples (all above ground tissue) were collected during the first week of herbivore exposure

Table 1

Mean physical and chemical attributes of study species for each site. For all attributes, n = 20, except for n = 10 (species samples pooled) for chemical analysis. NSS denotes insufficient sample material. Units of measure expressed as follows: Plant height in cm, H_2O : % dry weight, leaf thickness in mm, LMA = leaf mass : area (mg mm^{-2}), tannin (total), Fibre (ADF), N, P, K, Na and Ca: % dry weight.

	Species	Height	H₂O	Thickness	LMA	Density	Tannin	Fibre	N	P	K	Na	Ca
	SITE 1												
1	Aira sp.	9.67	69.2	0.29	45	154	0.55	47.2	0.62	0.03	0.06	0.15	0.19
2	Astrostipa compressa	15.2	62.3	0.32	979	2990	0.50	NSS	2.10	0.25	1.52	0.21	0.38
3	Dasypogon bromeliifolius	14.2	68.8	3.14	249	90	2.36	44.1	1.39	0.04	0.87	0.16	0.20
4	Gladiolus caryophyllaceus	19.3	83.1	0.58	128	228	0.60	36.6	1.21	0.10	1.76	0.03	0.79
5	Haemodorum spicatum	47.5	85.0	0.66	158	249	0.60	28.9	2.52	0.15	3.46	0.12	0.72
6	Hypochaeris sp.	19.9	85.5	0.2	58	289	0.10	NSS	1.91	0.09	1.31	0.92	1.51
7	Trachymene pilosa	7.25	85.0	0.4	50	124	2.20	NSS	2.01	0.14	1.30	0.92	1.41
8	Ursinia anthemoides	20.5	75.2	0.25	81	314	0.77	33.9	2.10	0.09	1.11	0.97	0.58
9	Waitzia suavolens	9.0	82.9	0.43	36	81	1.20	48.8	0.78	0.04	1.37	0.46	0.69
10	Xanthorrhoea preissii	67.8	64.7	2.15	675	318	0.73	41.3	0.95	0.04	0.74	0.07	0.74
	SITE 2												
1	Aira sp.	8.9	69.2	0.29	45	154	0.55	47.2	0.62	0.03	0.06	0.15	0.19
2	Chaemascilla corymbosa	6.7	81.8	0.33	42	128	NSS	NSS	2.66	0.13	2.14	0.29	0.34
3	Cyathochaeta avenaceae	6.7	56.6	1.87	381	201	1.00	43.6	1.11	0.04	0.84	0.21	0.14
4	Gladiolus caryophyllaceus	15.7	83.1	0.58	128	228	0.60	36.6	1.21	0.10	1.76	0.03	0.79
5	Hypochaeris sp.	11.5	85.5	0.2	58	289	0.10	NSS	1.91	0.09	1.31	0.92	1.51
6	Kennedia prostrata	2.8	69.7	0.22	85	385	1.53	31.6	2.94	0.13	1.23	0.23	1.22
7	Lyperanthus serratus	9.9	86.8	0.44	168	391	5.50	22.2	2.49	0.12	2.22	0.57	0.28
8	Angianthus humifusus	1.8	91.3	1.14	49	43	NSS	NSS	NSS	NSS	NSS	NSS	NSS
9	Waitzia suavolens	9.1	82.9	0.43	36	81	1.20	48.8	0.78	0.04	1.37	0.46	0.69
10	Xanthorrhoea preissii	101.6	64.7	2.15	675	318	0.73	41.3	0.95	0.04	0.74	0.07	0.74
	SITE 3												
1	Aira sp.	7.8	69.2	0.29	45	154	0.55	47.2	0.62	0.03	0.06	0.15	0.19
2	Astrostipa compressa	16.3	62.3	0.32	979	2990	0.50	NSS	2.10	0.25	1.52	0.21	0.38
3	Burchardia umbellata	26.3	81.4	0.4	74	239	1.33	41.2	1.63	0.09	1.65	0.14	0.33
4	Gladiolus caryophyllaceus	11.85	83.1	0.58	128	228	0.60	36.6	1.21	0.10	1.76	0.03	0.79
5	Desmocladus flexuosa	7.2	47.6	1.16	549	475	1.05	32.2	0.97	0.02	0.68	0.21	0.30
6	Haemodorum spicatum	55.3	85.0	0.66	158	249	0.60	28.9	2.52	0.14	3.45	0.12	0.72
7	Pattersonia occidentalis	17.4	66.9	1.22	267	225	1.13	48.6	0.94	0.03	1.53	0.08	0.32
8	Podotheca chrysantha	19.5	88.9	0.41	70	173	1.03	27.3	2.55	1.12	0.92	1.63	2.92
9	Trachymene pilosa	6.2	85.0	0.4	50	124	2.20	NSS	2.01	0.14	1.30	0.92	1.41
10	Ursinia anthemoides	18.1	75.2	0.25	81	214	0.77	33.9	2.10	0.09	1.11	0.97	0.58

from protected sites to ensure no influence of herbivory on plant chemistry. These were dried at 60° C for 48 hours in an air-forced oven. Numbers of plants used varied according to species type; for some small annual species, sufficient samples could not be collected in the vicinity of the trials to provide the minimal mass required for some analysis. All samples were milled using a coffee grinder and run through a Culatti® beater mill with 1 mm gauze sieve. Attributes analysed were selected due to their relative importance in regards to palatability (Hanley 1998).

Nitrogen, potassium and phosphorus

Nitrogen content of whole plants was determined using 200 mg of plant sample digested with H_2SO_4 and H_2O_2 in the presence of salicylic acid (Bradstreet 1965), and analysed using a Technicon segmented analyser using Berthelot colorimetric determination (Searle 1984). Determination of total P and K were completed using similar methods, although molybdate/vanadate colorimetric reaction and flame emission spectrometry (Varley 1966) were used respectively.

Acid detergent fibre (ADF)

ADF gives a combined measure of cellulose, lignin and cutin. About 200 mg of plant material was simmered in an acidic detergent solution for 1 hour, filtered on a coarse sintered glass crucible and washed with acetone to prevent possible complex formation from the interaction of tannins and proteins, forming insoluble precipitates that elevate ADF values. Weight of dry residue gave ADF, allowing for ash content. AOAC (973.18) and RACI (03–01) methods were used.

Total tannins

200 mg of plant material was extracted in 70% acetone and tumbled overnight. 200 mL supernatant aliquots were complexed with 5 mL deionised water, 12.5 mL of 200 g. L^{-1} Na_2CO_3 and 2.5 mL of 50% Folin Ciocalteu reagent. Samples were stood for 30 minutes then centrifuged at 3000 rpm for 10 minutes. Absorbance was read at 725 nm on a UV-visible Spectrophotometer. Values were plotted against a standard curve produced from tannic acid analysis. Results were expressed as tannic acid equivalents.

Data analysis

Log-likelihood analyses were completed for surrounding survey data to test consistency of grazing between sites and effect of plant spinescence on herbivory. Alive/dead status of protected and exposed plants were compared using log-likelihood analysis. *P* values are given without Bonferroni correction (Rothman 1990). Correlations between plant damage and selected plant traits were determined using Microsoft Excel for Mac (2002) after arcsine transformation. Densities of study species at each site were analysed in relation to time (2001 and 2003) and position (exposed/protected) using univariate GLM ANOVA by SPSS 11 for Mac OS X (SPSS Inc 2002). Plant attributes most closely correlated to plant damage at each site were determined using canonical variance analysis (CVA). Plants were assigned to one of three damage classes: site 1: 0%, 1–9%, 10–100%; site 2: 0%, 1–10%, 11–100%; site 3: 0%, 1–20%, 21–100%. Damage classes differed between sites due to differences in the magnitude of herbivory experienced at each location. Distributions of non-normal attributes were transformed as follows: density (log), height (sqrt), leaf thickness (log), tannin (log) and K (sqrt). Due to insufficient sample material for tannin analysis of

Chaemascilla (site 2) and lack of correlation of this compound with other measured plant attributes, an average tannin value for all species was calculated and used for CVA to allow the inclusion of the species.

Results

Surrounding herbivory

Over 100 species of plants are included in the diet of native vertebrate herbivores in southwestern Australia (Appendix 1). Legumes including *Acacia*, *Bossiaea*, *Daviesia* and *Gastrolobium* feature strongly, as do many of the Haemodoraceae, Cyperaceae and Restionaceae. Percentages of plants eaten varied markedly for species surveyed in the surrounds of the study sites, although trends for species and family groups often agreed with those from the literature and listed in Appendix 1. Grass-like genera of the families Cyperaceae, Haemodoraceae, Restionaceae and Xanthorrhoeaceae commonly showed herbivore damage. *Dasypogon bromeliifolius* and *Patersonia occidentalis* were two exceptions of grass-like species that were not selected by herbivores (Appendix 2). All members of the Myrtaceae were avoided, as were

Table 2

Log likelihood ratio results for alive/dead in relation to protection/exposure to herbivores. For all comparisons, *df* = 1, n = 20, except for Site 2, *Aira* sp. n= 18, *Hypochaeris* sp. = 19 and *Xanthorrhoea* = 9. *P* values denoted as * < 0.05, ** < 0.01, *** < 0.001.

Species	Alive Protected	Exposed	Dead Protected	Exposed	χ^2
Site 1					
Aira sp.	0	0	20	20	0.0
Austrostipa compressa	9	0	11	20	15.1***
Dasypogon bromeliifolius	20	20	0	0	0.0
Gladiolus caryophyllaceus	2	17	18	3	25.4***
Haemodorum spicatum	20	20	0	0	0.0
Hypochaeris sp.	5	0	15	20	7.6**
Trachymene pilosa	0	0	20	20	0.0
Ursinia anthemoides	0	0	20	20	0.0
Waitzia suaveolens	0	0	20	20	0.0
Xanthorrhoea preissii	20	20	0	0	0.0
Site 2					
Aira sp.	0	0	19	18	0.0
Angianthus humifusus	0	0	20	20	0.0
Chaemascilla corymbosa	0	0	20	20	0.0
Cyathochaeata avenaceae	19	20	1	0	1.4
Gladiolus caryophyllaceus	15	18	5	2	88.1***
Hypochaeris sp.	0	2	20	17	3.0
Kennedia prostrata	20	20	0	0	0.0
Lyperanthus serratus	17	17	1	3	0.9
Waitzia suaveolens	0	0	20	20	0.0
Xanthorrhoea preissii	12	9	0	0	0.0
Site 3					
Aira sp.	3	0	17	20	4.3*
Austrostipa compressa	9	2	11	18	6.5*
Burchardia umbellata	10	17	10	3	5.8*
Gladiolus caryophyllaceus	9	6	11	14	0.9
Alexgeorgia nitens	19	18	1	2	0.4
Haemodorum spicatum	20	20	0	0	0.0
Pattersonia occidentalis	20	20	0	0	0.0
Podotheca chrysantha	13	1	7	19	17.9***
Trachymene pilosa	2	0	18	20	2.9
Ursinia anthemoides	4	0	16	20	6.0

many of the Proteaceae with the exception of *Banksia attenuata* and *Persoonia saccata*. The exotic *Carpobrotus edulis* was grazed relatively heavily at site 2, although for sites 1 and 3 none showed any sign of damage.

Plant mortality

Hypochaeris sp. and *A. compressa* showed significantly higher rates of death in exposed plots than in those protected from herbivores (Table 2). At site 2, *G. caryophyllaceus* was the only species significantly affected by exposure. A number of species showed high mortality rates at site 3, including *U. anthemoides, P. chrysantha, B. umbellata, A. compressa* and *Aira* sp.

Plant density

Average densities of each of the ten study species per plot in the short- and long- term are given in Table 3. Plant density values after a short period (four weeks) of herbivore exposure were almost identical to pre-exposure values. Despite herbivore access, a high percentage of marked plants remained after herbivory, often as remnant stems, thus density was a poor indication of true herbivore activity after this time and was not included in further analyses. There was no relationship between the abundance of plant species in the environment and herbivory ($R = 0.333$).

Percentages of species showing herbivore damage differed greatly at each site after 4 weeks exposure (Table 3). *Austrostipa* was targeted at site 1 relative to other species (35% damaged). At site 2, *Waitzia* suffered the greatest of all the study species (35%), together with grassy *Aira* (30%). Grasses showed the greatest levels of damage at site 3, with *Aira* (50%), *Gladiolus* (30%) and *Desmocladus* (30%) commonly selected. *Podotheca* was also favoured (30%).

Damage values for plants surrounding each study site suggested herbivory differed greatly between plant species and sites. Of the individuals examined, the greatest proportions showing signs of herbivory were from families with typically grass-like morphologies: the Dasypogonaceae, Haemodoraceae and Restionaceae. The leguminous Fabaceae were one exception, with *Jacksonia*

Table 3

Densities of plants (No. per m², mean (SE)) at the beginning of the survey (2001), related to percentage of plants showing herbivore damage after four weeks of exposure and densities after 2 years (2003). Survey site for protected 2003 located approximately 20m from original site due to fencing amendment to facilitate ongoing herbivore monitoring.

Species	Plant density 2001		% Plants damaged	Plant density 2003	
SITE 1	Exposed	Protected	Exposed	Exposed	Protected
Aira sp.	201 (154)	1373 (878)	0	29595 (13005)	12620 (8142)
Austrostipa compressa	3793 (1346)	3372 (645.1)	35	1141 (357)	77 (28)
Dasypogon bromeliifolius	666 (329)	144 (66)	5	66 (12)	39 (10)
Gladiolus caryophyllaceus	726 (333)	936 (483)	0	41 (7)	162 (110)
Haemodorum spicatum	53 (18)	45 (5)	0	37 (7)	35 (3)
Hypochaeris sp.	69 (17)	638 (417)	0	488 (297)	14175 (10507)
Trachymene pilosa	1304 (944)	217 (63)	0	2693 (1141)	3605 (1738)
Ursinia anthemoides	174 (126)	1716 (1637)	5	675 (354)	1864 (694)
Waitzia suaveolens	280 (187)	1493 (725)	10	1519 (433)	6966 (5230)
Xanthorrhoea preissii	43 (5)	119 (37)	0	45 (11)	104 (44)
SITE 2					
Aira sp.	463 (438)	159 (108)	30	3856 (2712)	142929 (125009)
Angianthus humifusus	61 (34)	155 (53)	0	7746 (3302)	25 (0)
Chaemascilla corymbosa	1357 (1293)	159 (70)	5	60 (20)	25 (0)
Cyathochaeta avenacea	13098 (4422)	12592 (4670)	0	18891 (6960)	561 (442)
Gladiolus caryophyllaceus	59 (15)	54 (10)	5	25 (0)	25 (0)
Hypochaeris sp.	51 (16)	39 (4)	5	770 (364)	10362 (4358)
Kennedia prostrata	46 (17)	40 (5)	25	25 (0)	3569 (3276)
Lyperanthus serratus	37 (7)	29 (4)	0	43 (15)	25 (0)
Waitzia suaveolens	140 (114)	86 (46)	35	395 (242)	29 (3)
Xanthorrhoea preissii	35 (4)	32 (7)	15	34 (9)	132 (102)
SITE 3					
Aira sp.	70 (28)	3154 (3118)	50	5831 (3801)	6873 (4792)
Austrostipa compressa	762 (301)	270 (144)	25	178 (87)	304 (238)
Burchardia umbellata	72 (6)	146 (51)	15	64 (19)	194 (80)
Gladiolus caryophyllaceus	1566 (499)	1292 (641)	30	164 (109)	144 (78)
Alexgeorgia nitens	2276 (1392)	2946 (1687)	30	1428 (978)	92 (19)
Haemodorum spicatum	90 (32)	56 (5)	0	119 (44)	35 (4)
Patersonia occidentalis	25 (0)	30 (3)	5	33 (6)	37 (4)
Podotheca chrysantha	37 (8)	81 (21)	30	10816 (3518)	7956 (7088)
Trachymene pilosa	116 (36)	390 (264)	5	2247 (919)	586 (511)
Ursinia anthemoides	125 (43)	466 (348)	0	625 (286)	191 (76)

and *Kennedia* commonly selected. Species of Myrtaceae were never selected.

Effects of herbivory and time

Time significantly affected the density of all genera with the exception of *Haemodorum*, *Trachymene* and *Xanthorrhoea*. Effects appeared highly variable between species, however, with some densities greater in exposed plots than protected, suggesting herbivory did not directly determine abundance (Table 4). The effect of exposure to herbivory upon species density was less than for time, having a significant influence upon *Austrostipa*, *Dasypogon* and *Hypochaeris*. An interaction effect was only noted for *Austrostipa* and *Xanthorrhoea*. Time was less influential upon density at site 2 than position, only effecting *Aira*, *Gladiolus* and *Hypochaeris* (increased density) and also *Cyathochaeta* (decreased density). Densities of *Aira*, *Cyathochaeta* and *Hypochaeris*, but not *Gladiolus*, were affected by exposure to herbivory. An interaction effect was evident for *Angianthus*, *Cyathochaeta* and *Hypochaeris*, with the densities of *Angianthus* and *Cyathochaeta* increasing significantly in

Table 4

Results of tests upon densities of plants in relation to position (protected/exposed) and time (year – 2001/2003). For all species df=3, univariate GLM ANOVA.

Species	P Position	Time	Interaction
Site 1			
Aira sp.	0.000	0.579	0.191
Austrostipa compressa	0.000	0.025	0.007
Dasypogon bromeliifolius	0.002	0.024	0.331
Gladiolus caryophyllaceus	0.001	0.325	0.585
Haemodorum spicatum	0.225	0.952	0.952
Hypochaeris sp.	0.012	0.028	0.479
Trachymene pilosa	0.072	0.884	0.210
Ursinia anthemoides	0.045	0.115	0.608
Waitzia suaveolens	0.015	0.114	0.433
Xanthorrhoea preissii	0.599	0.599	0.011
Site 2			
Aira sp.	0.005	0.703	0.840
Angianthus humifusus	0.152	0.045	0.002
Chaemascilla corymbosa	0.068	0.413	0.794
Cyathochaeata avenacea	0.009	0.003	0.001
Gladiolus caryophyllaceus	0.000	0.899	0.876
Hypochaeris sp.	0.000	0.008	0.005
Kennedia prostrata	0.275	0.089	0.100
Lyperanthus serratus	0.799	0.119	0.603
Waitzia suaveolens	0.550	0.101	0.065
Xanthorrhoea preissii	0.470	0.530	0.335
Site 3			
Aira sp.	0.009	0.725	0.633
Austrostipa compressa	0.150	0.399	0.342
Burchardia umbellata	0.887	0.056	0.553
Gladiolus caryophyllaceus	0.000	0.826	0.549
Alexgeorgia nitens	0.022	0.585	0.078
Haemodorum spicatum	0.533	0.032	0.224
Pattersonia occidentalis	0.069	0.206	0.951
Podotheca chrysantha	0.000	0.477	0.066
Trachymene pilosa	0.052	0.203	0.035
Ursinia anthemoides	0.372	0.925	0.229

Table 5

Ranking of correlation coefficients from strongest to weakest for plant attributes with percentage of plants eaten for each site after 4 weeks exposure. Symbol in brackets denotes positive or negative relationship. No correlations were significant ($P > 0.05$, $df = 8$ for sites 1 and 3, $df = 7$ for site 2).

Rank	Site 1	Site 2	Site 3
1	Na (-)	H_2O (+)	Leaf density (-)
2	H_2O (+)	Leaf thickness (-)	Na (-)
3	LMA (-)	Na (+)	Plant density (+)
4	Leaf thickness (-)	Plant height (-)	LMA (+)
5	N (-)	Plant density (-)	P (-)
6	Ca (-)	Phenolics (+)	N (-)
7	Phenolics (-)	LMA (-)	Phenolics (-)
8	Plant density (-)	Ca (+)	Ca (-)
9	Leaf density (-)	P (+)	H_2O (+)
10	P (-)	N (-)	Leaf thickness (-)
11	Plant height (-)	Density (-)	Plant height (+)

the exposed area over time, while decreasing in the protected area. For *Hypochaeris*, density increased significantly in the exposed and protected sites with time. Fewer effects were evident at site 3. Time affected densities of *Aira* and *Alexgeorgia* (decreased density) and *Gladiolus* and *Podotheca* (increased density), although position had little effect, with the exception of *Haemodorum*. An interaction between position and time was noted for *Trachymene*. *Austrostipa* was not influenced by either variable.

Plant attributes

A rank of correlations of plant attributes with plant damage was constructed by completing Principal Components Analysis for species at each site (Podani 1994). Plant damage was not significantly correlated with any facet of plant morphology at any site, and ranks varied between sites (Table 5). Sodium had a negative influence on selection at sites and 1 and 3, although for site 2 this trend was absent. This trend was similar for calcium, although the influence of this salt was less profound than with sodium. Moisture content had the most influence upon selection at site 2, although for site 3, leaf density had the greatest effect. Plant height had the least influence on selection at sites 1 and 3, while leaf density was of least influence at site 2. Plant density had little effect on selection at any site.

Discussion

Feeding preferences of macropods at Whiteman Park were similar to those of many native herbivores in southwestern Australia (Bell 1994; Shepherd *et al.* 1997; Bell *et al.* 1987). Tables 1 and 2 highlighted a preference for grass-like species, while Myrtaceous species were considered less palatable. Tolerance for aromatic species such as *Corymbia calophylla* and *Eucalyptus marginata* is prevalent for some possum species (Appendix 1) and has also been reported for *M. eugenii* and *M. irma*, but not *M. fuliginosus* (Shepherd *et al.* 1997; Wann & Bell 1997). Similarly, feeding upon *C. calophylla* and *E. marginata* was never observed at Whiteman Park throughout the duration of the study.

Density comparisons two years after fire were very useful in demonstrating the long-term impact of selective feeding. Of particular interest were changes in populations of weed species, with densities of many species significantly affected by time. The direction of the effect (i.e. increase or decrease in density) and ecology of individual species was an important consideration when assessing these results. For some species (e.g. *Aira*, site 1, 2003), exposed plots had greatest densities, suggesting microsite differences, such as light availability or differential seed set in previous years, may be more influential than herbivore activity, although sites were selected where possible to minimise such extrinsic factors. Alternatively, *Aira* may benefit from macropod feeding upon other species, reducing competitive impacts of surrounding vegetation. Differences in density between exposed and protected plots at the beginning of the study (Table 3) further emphasize this potential for species density to vary greatly at the microsite level.

Effects of herbivory and time were of particular interest in regards to fire ephemeral species, such as *Austrostipa compressa*. *A. compressa* density decreased significantly with time since fire at site 1, as has been observed in other systems (Baird 1984). Germination and flowering of this species are typically stimulated by fire, and it appeared to make up an important component of the kangaroo diet following fire relative to other species (35% plants damaged after four weeks' exposure). With time, however, herbivory did not appear to have a detrimental effect on density of the species, with values in exposed plots significantly greater than in protected plots in 2003. Effects were absent at site 3, although overall densities for the species at this site were less overall throughout the study. Dry conditions observed within the study area on the dune slope at site 3 may have outweighed any herbivore or time effects on more sensitive plant species. For sites 2 and 3, mortality of species was rarely increased by macropod feeding, and with the exception of *Austrostipa*, those significantly affected were primarily introduced species. Harsh environmental conditions at site 3, where plants were exposed on the dune crest, may have contributed simultaneously with herbivory to increase mortality relative to other sites.

Examination of death rates of species in protected and exposed sites revealed that non-geophytic resprouters tended not to be eaten, while annuals were preferentially selected. Among the sites, the mortality of *Cyathochaeta*, *Dasypogon*, *Patersonia* and *Xanthorrhoea* were low, with species usually exempt from browsing. This contrasted with many of the smaller annuals and geophytes, including *Aira*, *Austrostipa*, *Hypochaeris* and *Podotheca*, where lower survival rates were attributed to macropod feeding. Perennials and shrubs, including *Desmocladus*, *Haemodorum* and *Kennedia*, were commonly grazed. Mortality of such species appeared unaffected by Macropod feeding, however, suggesting plant growth form is a major influence in determining the herbivory outcomes in many instances.

Densities of short-lived annuals, particularly after the fire, typically exceeded longer-lived species. Shorter-lived annuals are typically fast growing, reproducing rapidly, and thus are available to herbivores for a short time in great abundance (personal observations).

Investment in herbivore defence may be minimal, with the individuals escaping in space and time (Briner & Frank 1998). While repeated grazing of many resprouters is observed to lead to their eventual death (Leigh & Holgate 1979; Wahungu *et al*. 1999), there appeared to be few long-lived species among the study selection with enhanced defence mechanisms such as secondary metabolites (e.g. tannins). *Dasypogon*, *Trachymene* and *Lyperanthus* had the greatest tannin levels, although all three have markedly different life strategies and suffered variable herbivore damage. With the exception of *Dasypogon* with serrated leaf margins, none of the species had physical defence mechanisms, suggesting other cues were driving macropod selection habits.

Correlation coefficients confirmed that the plant attributes analysed had little influence on feeding selection. The lack of correlation between plant density and percentage eaten emphasizes the highly selective feeding behaviour of macropods at the reserve. Certain plants, especially grasses, *Austrostipa*, *Desmocladus* and *Aira*, were favoured over more abundant, larger species (Appendices 1 and 2). At site 1, however, *Aira* escaped attention, possibly due to the high density of palatable alternatives such as *Austrostipa*. Introduced species featured strongly, indicating weeds are equally subject as native plant species to macropod feeding. Macropod grazing may act to reduce weed cover to a significant extent in some areas, although as shown by differences in grazing damage of *Aira* between the three sites, feeding activity was independent of weed density, contrasting with the findings of Mattiske Consulting (1995).

It is likely that pre-European fire regimes encouraged the regrowth of undefended seedling species, with fire often affecting large tracts of land (Flannery 1994). Such vast areas were unlikely to be reinhabited by vertebrates for some time, allowing substantial development of small herbaceous species, as well as larger resprouters, providing cover for smaller recruits. Although fire regimes were variable throughout the continent, a general reduction in the size and number of fires since European settlement typically facilitates rapid movement of large herbivores into post-fire areas. An increase in the effects of herbivory are therefore inevitable, with plants unable to evolve functional defensive strategies in such a short time. Effects are typically more significant to some plant species relative than others, which has been a key finding of my study. Understanding the factors influencing mammalian browsing can facilitate the development of management strategies. Current fire management regimes typically result in the burning of smaller areas, which are often reinhabited by herbivores within days. The ability of kangaroos to feed on lush post-fire growth, coupled with their increase in numbers in these remaining habitats with the availability of free water, undoubtedly impacts upon post-fire recruitment of species with little or no defence strategy. While herbivory appears to have a greater influence upon species density than fire, outcomes are highly species dependent. The selection of a number of weed species in the post-fire diet of macropods must also assist in native regeneration to some extent, reducing competition and decreasing fuel loads over time.

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Appendix 1

List of known food plants of Western Australian native marsupials. Leaf types denoted as spinescent = S, non-spinescent = NS; spinescence determined from Perth Flora (1987) and B. Lamont (pers. obs.). Methods of detection as food source denoted as F = faecal analysis, S = stomach content analysis, O = observed eating, P = plant damage. Native herbivores denoted as E = *Macropus eugenii* (tammar wallaby), F = *M. fuliginosus* (western grey kangaroo), I = *M. irma* (black-gloved or brush wallaby), P = *Pseudocheirus occidentalis* (western ring-tail possum), T = *Trichosurus vulpecula* (common brush-tail possum). Reference sources denoted as 1 = Halford, Bell & Loneragan (1984), 2 = Bell (1994), 3 = Shepherd, Wardell-Johnson, Loneragan and Bell (1997), 4 = Bell, Moredoundt & Loneragan (1987), 5 = Wann & Bell (1997). Exotic species denoted by *.

Plant species	Family	Woody shrub (w), Non-woody shrub (n), Grass-like (g)	Spinescent (S), Non-spinescent (N)	Native herbivore	Method of detection	Reference
Acacia celastrifolia	Mimosaceae	w	N	F	F	1, 2
Acacia extensa	Mimosaceae	w	N	F		2
Acacia pulchella	Mimosaceae	w	S	F, E	F	2, 3
Acacia rostellifera	Mimosaceae	w	N	E	F, S, O	2, 4
Acacia stenoptera	Mimosaceae	n	S	I	F	5
Adenanthos cygnorum	Proteaceae	w	N	F	F, P	1, 2, 5
Alexgeorgea nitens	Restionaceae	g	S	I	F	5
Allocasuarina sp.	Casuarinaceae	w	N	F		2
Allocasuarina sp.	Casuarinaceae	w	N	F	F	1
Anthocercis littorea	Solanaceae	w	N	F	P	1, 2
Arnocrinum preissii	Anthericaceae	g	N	I	F	5
*Ashodelus fistulosus**	Asphodelaceae	g	N	E	F, S, O	2, 3
*Asparagus asparagoides**	Asparagaceae	n	N	E	F, S, O	2, 4
Astroloma ciliatum	Epacridaceae	w	S	F	F	2, 3
Austrotipa flavescens	Poaceae	g	N	E		2
Austrotipa sp.	Poaceae	g	N	F	F	5
Baeckaea camphorosmae	Myrtaceae	w	N	F		2
Beaufortia elegans	Myrtaceae	w	N	I	F	5
Billardiera variifolia	Pittosporaceae	n	N	F	F	3
Boronia spathulata	Rutaceae	n	N	F, I	F	3, 5
Bossiaea eriocarpa	Fabaceae	n	N	F	F, P	1, 2, 5
Bossiaea linophylla	Fabaceae	n	N	E, F		2
Bossiaea ornata	Fabaceae	n	N	F, I	F	2, 3, 5
Burchardia multiflora	Colchicaceae	g	N	F	P	1, 2
Callitris preissii	Cupressaceae	w	N	E	F, S	4, 2
Calothamnus sanguineus	Myrtaceae	w	N	F	F, P	1, 2
Carprobrotus edulis	Aiozaceae	n	N	F, I	F	5
Cassytha sp.	Lauraceae	n	N	E, I	F	3
Centaurium erythraea	Gentianaceae	n	N	E	F	3
Clematis pubescens	Ranunculaceae	n	N	E, F		2
Conostylis setigera	Haemodoraceae	g	N	F	F, P	1, 2
Corymbia calophylla	Myrtaceae	w	N	E, F, P, T	F	3
Corynotheca micrantha	Anthericaceae	g	N	F, I	F	5
Cyathochaeta avenacea	Cyperaceae	g	N	E		2
*Cynodon dactylon**	Poaceae	g	N	F, I	F	5
Dampiera lavandulacea	Goodeniaceae	n	N	F	F, P	1, 2
Dampiera linearis	Goodeniaceae	n	N	F, I	F	5
Daviesia decurrens	Fabaceae	n	S	F	F	1, 2
Daviesia gracilis	Fabaceae	n	S	F	F,P	1
Daviesia preissii	Fabaceae	n	S	F	F	2, 3
Desmocladus fasciculata	Restionaceae	g	N	F		2
Desmocladus flexuosa	Restionaceae	g	N	F	F	1, 5
Dianella revoluta	Phormiaceae	g	N	F	P	1, 2
Dichopogon sp.	Anthericaceae	g	N	F	P	1
Dicotyledon sp.			N	F, I	F	5
Drosera spp.	Droseraceae	n	N	F	P	1
Dryandra carduacea	Proteaceae	w	S	F	F, P	1, 2
Ehrharta calycina	Poaceae	g	N	F, I	F	5
Eremophila glabra	Myoporaceae	w	N	E	F, S	4, 2
Eucalyptus marginata	Myrtaceae	w	N	E, I, P, T	F	5, 3
Gastrolobium bilobum	Fabaceae	w	N	E, F, I, T	F	3
Gastrolobium calycinum	Fabaceae	w	S	F	F, P	1, 2
Gastrolobium trilobum	Fabaceae	w	S	F	F, P	1, 2
Glischrocaryon aureum	Haloragaceae	n	N	F	F, P	1, 2
Gompholobium preissii	Fabaceae	w	N	F	F	1, 2
Gyrostemon subnudus	Gyrostemanaceae	n	N	F	P	1, 2
Hakea ambigua	Proteaceae	w	N	F	F	1, 2
Hakea lissocarpha	Proteaceae	w	S	E, F, I, T	F	3

Appendix 1 (cont.)

Plant species	Family	Woody shrub (w), Non-woody shrub (n), Grass-like (g)	Spinescent (S), Non-spinescent (N)	Native herbivore	Method of detection	Reference
Hakea trifurcata	Proteaceae	w	S	F	F, P	1, 2
Hakea undulata	Proteaceae	w	S	F	F	1, 2
Hibbertia cunninghamii	Dilleniaceae	w	N	E		2
Hibbertia racemosa	Dilleniaceae	w	N	F		2
Hypocalymma angustifolium	Myrtaceae	w	N	E		2
Jacksonia furcellata	Fabaceae	w	S	F	F	5
Jacksonia restioides	Fabaceae	n	N	F	F, P	1, 2
Juncus pallidus	Juncaceae	g	N	E, F, I	F	3, 2
Kennedia carinata	Fabaceae	n	N	F	F	3
Lasiopetalum molle	Sterculiaceae	n	N	F	P	1, 2
Lasiopetalum oppositifolium	Sterculiaceae	n	N	E	F	4, 2
Lepidosperma angustatum	Cyperaceae	g	S	F	F	3
Lepidosperma scabrum	Cyperaceae	g	S	F	F, P	1, 2
Lepidosperma tenue	Cyperaceae	g	S	E, F	F	3
Leptomeria cunninghamii	Santalaceae	n	N	E	F	3
Leucopogon capitellatus	Epacridaceae	w	S	E, F, I	F	2
Leucopogon conosteophioides	Epacridaceae	w	S	F, I	F	5
Leucopogon pulchellus	Epacridaceae	w	N	F		2
Leucopogon sp.	Epacridaceae	w	N	F, I	F	5
Leucopogon verticillatus	Epacridaceae	w	N	E, F, I	F	2, 3
Lomandra effusa	Haemodoraceae	g	N	F	F, P	1, 2
Lomandra hermaphrodita	Haemodoraceae	g	N	F	F, P	1, 2
Lomandra preissii	Haemodoraceae	g	N	F		2
Lomandra sericea	Haemodoraceae	g	N	E, F, I	F	3
Lomandra sonderii	Haemodoraceae	g	N	E	F	3
Lomandra sp.	Haemodoraceae	g	N	F	F	2, 3
Loxocarya sp.	Restionaceae	g	N	E, F, I	F	3
Lysinema ciliatum	Epacridaceae	w	N	I	F	5
Macrozamia riedlei	Zamiaceae	w	S	F, I	F	2, 5
Melaleuca viminea	Myrtaceae	w	N	F, I	F	3
Mesomalaena stygia	Cyperaceae	g	S	I	F	5
Mesomalaena tetragona	Cyperaceae	g	S	F		2
Mirbelia ramulosa	Fabaceae	n	N	F	F, P	1, 2
Monocotyledon sp.		g		F, I		5
Native grasses (non-flowering)		g	N	F	P	1
Neurachne alopecuroidea	Poaceae	g	N	F	F, P	1, 2, 3
Notodanthonia setacea	Poaceae	g	N	E, F, I	F	5, 3
Nuytsia floribunda	Loranthaceae	n	N	F, I	F	5
Opercularia hispidula	Rubiaceae	n	N	E, F, I	F	3
Opercularia vaginata	Rubiaceae	n	N	F	F, P	1, 2
Oxylobium capitatum	Fabaceae	w	S	F, I	F	5
Patersonia occidentalis	Iridaceae	g	N	F, I	F	5
Persoonia longifolia	Proteaceae	w	N	F		2
Petrophile serruriae	Proteaceae	w	S	F	P	1, 2
Phyllanthus calycinus	Rosaceae	n	N	E	F, S, O	2, 4
Schoenus cyperacea	Cyperaceae	g	N	E		2
Solanum symonii	Solanaceae	n	N	E	F, S, O	2, 4
Stylidium affine	Stylidiaceae	n	N	F	F, O	2, 4
Stypandra imbricata	Phormiaceae	g	N	F	F, P	1, 2
Tetraria octandra	Cyperaceae	g	N	F	F	1, 2
Tetrarrhena laevis	Poaceae	g	N	F	F	3
Tetratheca confertifolia	Tremandraceae	n	N	E, F	P, F	1, 2
Thomasia cognata	Sterculiaceae	n	N	F	F, O	2, 4
Trachyandra divaricata*	Asphodelaceae	g	N	E	F, S	2, 4
Tribonanthes uniflora	Haemodoraceae	g	N	F	P	1, 2
Tricoryne elatior	Anthericaceae	g	N	F, I	F	5
Xanthorrhoea preissii	Xanthorrhoeaceae	g	S	F, I	F	1, 5

Appendix 2

Naturally regenerating plant species observed in 2 km radius of each study site. A maximum of 15 plants were examined where possible and macropod damage noted. N : non-spinescent foliage, S : spinescent foliage.

Family	Species	Spinescence	Site	No. plants examined	Plants eaten (%)
Aiozaceae	*Carpobrotus edulis*	N	1	15	0
Aiozaceae	*Carpobrotus edulis*	N	2	15	47
Aiozaceae	*Carpobrotus edulis*	N	3	15	0
Cyperaceae	*Cyathochaeta avenacea*	N	2	15	67
Dasypogonaceae	*Dasypogon bromeliifolius*	S	1	15	0
Dasypogonaceae	*Dasypogon bromeliifolius*	S	2	15	0
Dasypogonaceae	*Dasypogon bromeliifolius*	S	3	15	0
Dasypogonaceae	*Lomandra caespitosa*	N	1	10	80
Dasypogonaceae	*Lomandra caespitosa*	N	2	15	53
Dasypogonaceae	*Lomandra caespitosa*	N	3	10	80
Dilleniaceae	*Hibbertia huegelii*	N	2	5	60
Dilleniaceae	*Hibbertia vaginata*	N	1	15	0
Dilleniaceae	*Hibbertia vaginata*	N	2	15	0
Dilleniaceae	*Hibbertia vaginata*	N	3	15	0
Epacridaceae	*Conostephium pendulum*	S	1	10	0
Epacridaceae	*Conostephium pendulum*	S	3	10	0
Fabaceae	*Jacksonia floribunda*	S	1	15	93
Fabaceae	*Jacksonia floribunda*	S	3	15	93
Fabaceae	*Jacksonia sternbergiana*	S	2	15	60
Fabaceae	*Kennedia prostrata*	N	2	13	69
Haemodoraceae	*Conostylis setigera*	N	2	15	80
Haemodoraceae	*Haemodorum spicatum*	N	1	15	46
Haemodoraceae	*Haemodorum spicatum*	N	2	15	13
Haemodoraceae	*Haemodorum spicatum*	N	3	15	46
Iridaceae	*Patersonia occidentalis*	N	1	15	0
Iridaceae	*Patersonia occidentalis*	N	2	15	0
Iridaceae	*Patersonia occidentalis*	N	3	15	0
Mimosaceae	*Acacia pulchella*	S	2	4	25
Myrtaceae	*Calytrix flavescens*	N	1	15	0
Myrtaceae	*Calytrix flavescens*	N	3	15	0
Myrtaceae	*Corymbia calophylla*	N	1	15	0
Myrtaceae	*Corymbia calophylla*	N	2	15	0
Myrtaceae	*Corymbia calophylla*	N	3	15	0
Myrtaceae	*Hypocalymma angustifolium*	N	1	15	0
Myrtaceae	*Hypocalymma angustifolium*	N	2	15	0
Myrtaceae	*Hypocalymma angustifolium*	N	3	15	0
Myrtaceae	*Melaleuca preissiana*	N	2	5	0
Myrtaceae	*Pericalymma ellipticum*	N	2	15	0
Myrtaceae	*Regelia ciliata*	N	1	15	0
Myrtaceae	*Regelia ciliata*	N	3	15	0
Myrtaceae	*Scholtzia involucrata*	N	1	9	0
Myrtaceae	*Scholtzia involucrata*	N	2	11	0
Myrtaceae	*Scholtzia involucrata*	N	3	9	0
Proteaceae	*Banksia attenuata*	S	1	15	27
Proteaceae	*Banksia attenuata*	S	3	15	27
Proteaceae	*Dryandra lindleyana*	S	1	15	0
Proteaceae	*Dryandra lindleyana*	S	3	15	0
Proteaceae	*Persoonia saccata*	S	2	4	25
Proteaceae	*Stirlingia latifolia*	N	1	15	0
Proteaceae	*Stirlingia latifolia*	N	3	15	0
Restionaceae	*Alexgeorgea nitens*	S	1	15	100
Restionaceae	*Alexgeorgea nitens*	S	3	15	100
Restionaceae	*Alexgeorgea sp.*	S	2	15	87
Restionaceae	*Lygenia barbata*	S	2	15	100
Restionaceae	*Lyginia barbata*	S	1	15	100
Restionaceae	*Lyginia barbata*	S	3	15	100
Rutaceae	*Philotheca spicatum*	N	2	15	0
Xanthorrhoeaceae	*Xanthorrhoea preissii*	S	1	15	13
Xanthorrhoeaceae	*Xanthorrhoea preissii*	S	2	15	20
Xanthorrhoeaceae	*Xanthorrhoea preissii*	S	3	15	13

Stygofauna in the Pilbara region, north-west Western Australia: a review

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Abstract

North-west Western Australia appears to contain one of the world's more diverse subterranean faunas and this paper summarises published literature about stygofauna of the Pilbara region, within north-west Western Australia. To date, 332 occurrences of 78 species from approximately 223 sites have been recorded. The stygofaunal species occur in an array of different groundwater environments including porous, karstic and fractured-rock aquifers, springs and hyporheic habitats. Sampling coverage has been highly skewed in terms of areal coverage and the different types of groundwater environments represented – 96 % of sampled sites are bores or wells, while springs and hyporheic habitats have rarely been sampled. The higher-level systematic diversity of the region is quite comprehensive in global terms, but the species-level taxonomy of most groups is still incomplete. There appears to be significant regional endemism in the Pilbara stygofauna, including some relict freshwater lineages. Karstic aquifers, karst springs and porous alluvial aquifers contain high species richness. This review confirms that the Pilbara is an important region for subterranean biodiversity.

Keywords: stygofauna, Pilbara

Introduction

This paper reviews current information on stygofauna in the Pilbara region of north-west Western Australia by providing an updated list of taxa and making some comparisons with adjacent regions. Since the last synopsis of stygofauna in the Pilbara region (Humphreys 2000a), 11 papers describing 47 new species and seven new locality records from the Pilbara (cf. 23 described Pilbara species up to 2000) have been published. This suggests that the Pilbara region is important for subterranean biodiversity. The review is apposite because in recent years there has been some conflict between ecological water requirements for groundwater-dependent ecosystems, including stygofauna, and groundwater abstraction or mine dewatering (Water & Rivers Commission 1996; Johnson & Wright 2001; Playford 2001).

Despite its arid setting, north-west Western Australia appears to contain one of the world's more diverse subterranean faunas, dominated by crustaceans and including many relict obligate groundwater species with affinities to Tethys, and to Pangaea and its derived landmasses (Humphreys 1993ab, 1999a, 2001a; Knott 1993). This rich stygofauna was initially discovered in the anchialine groundwater system at Cape Range (Whitley 1945; Mees 1962; Humphreys & Adams 1991), subsequently on Barrow Island (Humphreys 2001b) and then in the Pilbara region (Poore & Humphreys 1998). As a consequence of earlier discovery and small land areas, the Cape Range (3,600 km²) and Barrow Island (324 km²) stygofaunas are reasonably well known and

taxonomically described, with a review and systematic lists in Humphreys (2000b). By contrast, since 2000 in the Pilbara region, descriptions have been published of Amphipoda (Bradbury 2000), Isopoda (Wilson 2003), Ostracoda (Karanovic & Marmonier 2002; Martens and Rossetti 2002; Karanovic 2003ab; Karanovic & Marmonier 2003; Karanovic 2005), Spelaeogriphacea (Poore & Humphreys 2003), and Copepoda (Karanovic 2004a; Karanovic 2006 in press). Taxonomic knowledge of Amphipoda has been augmented by molecular studies that investigated incongruence between morphology and molecular markers (Finston et al. 2004), and geographic patterns of genetic diversity (Finston and Johnson 2004). In addition, Pinder (2001) recorded undescribed species of phreodrilid oligochaetes, and there has been a substantial amount of recent collecting in the Pilbara region, results of which are unpublished. To the south of the Pilbara region, stygofauna have been discovered in the Murchison and Gascoyne regions (Humphreys 1999a; Watts and Humphreys 1999; Humphreys 2001a; Leys et al. 2003), and to the northeast, the Kimberley is proving to contain relictual lineages (Wilson & Ponder 1992), gondwanan relicts (Wilson & Keable 1999) and endemic taxa (Cho et al. 2005) (Figure 1).

Description of the Pilbara region

The Pilbara IBRA (Interim Biogeographic Region of Australia) region (20–24° S and 115–122° E) covers an area of approximately 178,000 km² in the arid north-west of Western Australia (Environment Australia 2000). The Pilbara IBRA region coincides, more or less, with the emergent part of the Pilbara Craton and encompasses five major hydrographic basins, from largest, Ashburton River Basin, De Grey River Basin, Fortescue River Basin, Port Hedland Coast Basin and Onslow Coast Basin
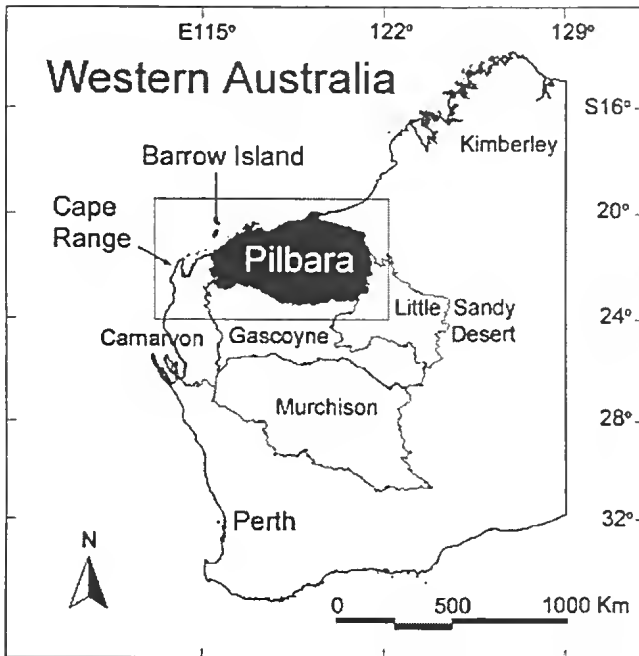
Figure 1. Western Australia showing the Pilbara IBRA region, and adjacent IBRA regions (Murchison, Carnarvon, Gascoyne, Little Sandy Desert), and other localities mentioned in the text (Cape Range, Barrow Island, Kimberley, Perth).

(Water and Rivers Commission 1996), although most of the Ashburton lies outside the IBRA region (Figures 1, 2). Because hydrography strongly influences the distribution of groundwater fauna, we are including the entire

Ashburton River Basin as part of the greater 'Pilbara region' (234, 886 km²), which is more or less synonymous with the 'Pilbara IBRA region'. Additionally, Barrow Island located 50 km off the Pilbara coast is part the Pilbara IBRA region, based on phytogeographic criteria, although geologically (along with Cape Range) it is part of the Northern Carnarvon (geologic) Basin (Hocking *et al.* 1987), so for the purposes of this review we are considering Barrow Island as separate from the Pilbara region.

Climate and physiography

The climate of the Pilbara region is Subtropical Dry, characterised by very low rainfall, high daytime temperature in summer and low winter minima (Gentilli 1972). Mean annual rainfall across the region ranges between 200 and 350 mm (mostly in summer), with high inter-annual variation associated with irregular tropical cyclones. For example, Tropical Cyclone Monty deposited 200–400 mm rain over the Pilbara region in March 2004 (http://www.bom.gov.au/weather/wa/cyclone/monty) and consequent flooding removed major bridges on the Robe and Maitland Rivers. Annual pan evaporation varies from 3200 mm near the coast to > 4000 mm inland (Bureau of Meteorology 1977). Although palaeoclimatic data are sparse, it is clear that aridity was well established at Cape Range by the Pliocene 5.3–2 million years ago (Ma) (Wyrwoll 1993). The long-term cumulative trend towards increasing aridity reached peak intensity during the Last Glacial Maximum (Wyrwoll 1979; van der Kaars & De Deckker 2002).
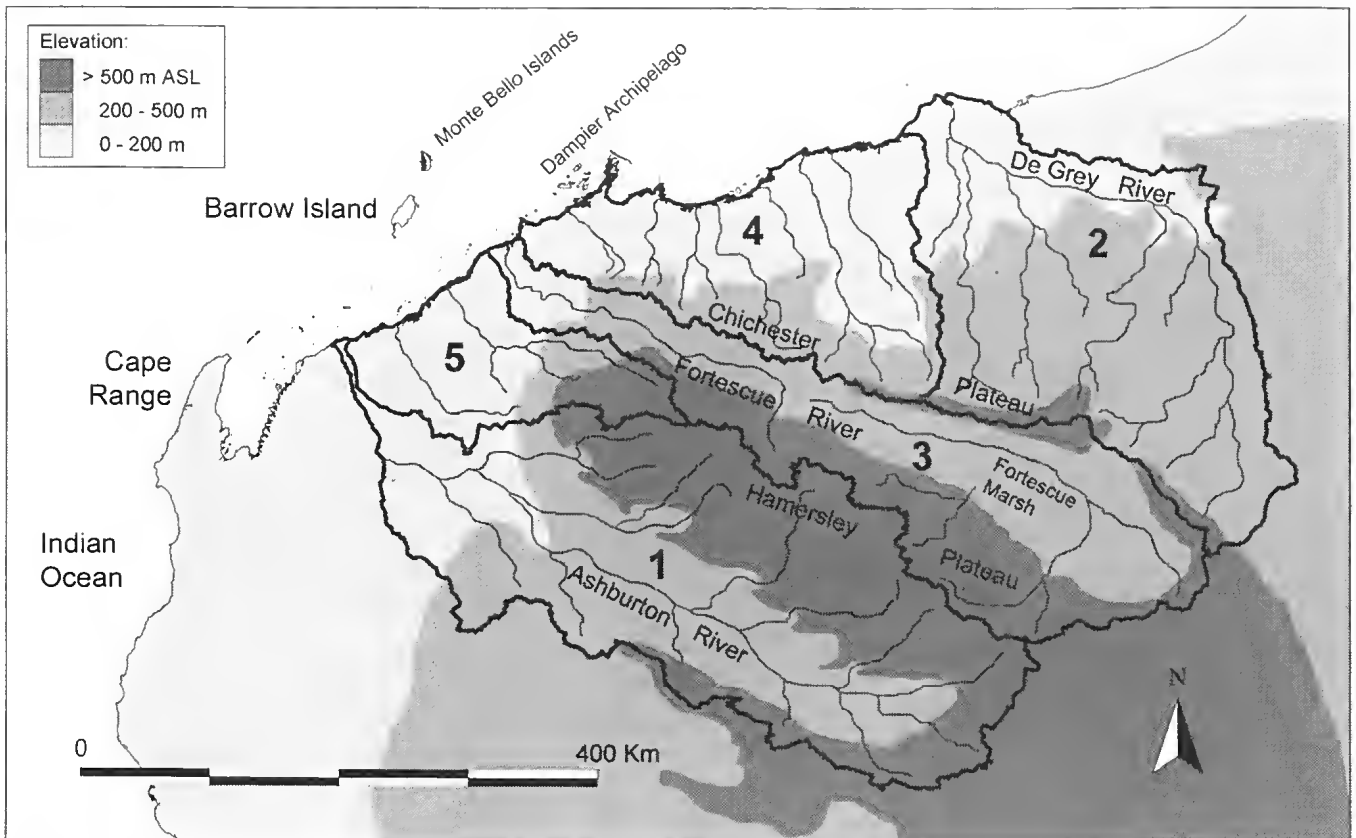

Figure 2. Pilbara region showing physiographic features mentioned in the text including elevation (metres above sea level), river drainage systems, and the five major hydrographic basins, numbered from largest: (1) Ashburton River Basin, (2) De Grey River Basin, (3) Fortescue River Basin, (4) Port Hedland Coast Basin, (5) Onslow Coast Basin (after Water and Rivers Commission 1996).

Much of the Pilbara region is a very old landscape, with the Pilbara Craton having remained more or less continually emergent since the Proterozoic (> 545 Ma), bordered by marine environments (including the Tethys Sea) from the Devonian (410–354 Ma) until the fragmentation of Gondwana in the Cretaceous (141–65 Ma) (Cockbain & Hocking 1990). The major physiographic features of the Craton are the Hamersley Plateau, the Fortescue River, and the Chichester Plateau and Range (Figure 2). The Hamersley Plateau, which coincides with the Central Pilbara iron ore region and contains the Hamersley Range that reaches an elevation of 1250 m above sea level (asl), is drained by the Ashburton and Fortescue Rivers, which flow northwest to the Indian Ocean. The Chichester Plateau, of more subdued relief (618 m asl), is drained to the north by numerous rivers in the De Grey and Port Hedland hydrographic basins. The river drainage systems have deeply dissected the margins of the Hamersley and Chichester Plateaus, but then follow broad low-gradient valleys across extensive lowlands to wide coastal plains. Development of the river drainage systems commenced during the Late Cretaceous to Early Tertiary (Beard 1973, 1998; van de Graaff *et al.* 1977). The river valleys accumulated sediments during the Cainozoic (65–0 Ma), including alluvium, colluvium, calcrete and Robe Pisolite (channel iron deposits) (van de Graaff *et al.* 1977). The coastal plain, and present coast formed during the Quaternary, are composed of riverine plains, deltas, tidal flats, coastal dunes and limestone barriers, relic deltas and archipelago/ria shores (Beard 1975; Hickman 1983; Semeniuk 1996).

Groundwater habitats

Groundwater occurs throughout the Pilbara region in the Precambrian basement rocks, Phanerozoic sedimentary basins and Cainozoic deposits. It originates from direct rainfall recharge over outcropping basement rocks and from infiltration of rainfall and runoff through Cainozoic deposits, especially during periodic flooding (Davidson 1975; Water and Rivers Commission 1996). Aquifers have been classified into three types by Johnson & Wright (2001): (1) unconsolidated sedimentary aquifers; (2) chemically-deposited aquifers; and (3) fractured-rock aquifers. Unconsolidated sedimentary aquifers comprise Cainozoic valley and coastal plain alluvium and colluvium, whilst chemically-deposited aquifers consist of calcrete or pisolitic limonite formed within valley-fill sequences. Fractured rock aquifers occur in Proterozoic and Archaean sedimentary and volcanic rocks, including dolomite, sandstone, shale, chert, banded-iron formation and basalt.

The highest yielding aquifers are contained within the alluvial aquifers on the coastal plains and the valley-fill aquifers within the Fortescue Valley and Hamersley Range where sequences of alluvium/colluvium, Millstream Dolomite, calcrete and Robe Pisolite have saturated thicknesses generally between 10 to 30 m (Water and Rivers Commission 1996; Johnson & Wright 2001). Major aquifers also occur in Proterozoic dolomites (Wittenoom Dolomite and Carawine Dolomite) that have been karstified and contain cavernous zones (Barnett & Commander 1985). Aquifers in other hard rocks rely on fracturing and jointing which may be locally significant in the Brockman and Marra Mamba Iron Formations and

the Hardey Sandstone (Johnson and Wright 2001). Inter-fluvial areas contain low yielding aquifers owing to shallow regolith cover, as do coastal flatlands which have high silt-clay fractions and low permeability away from the river deltas (Davidson 1975). Granitic rocks usually contain low-yielding aquifers unless deeply weathered.

Different geology and aquifer types yield particular groundwater habitats. The unconsolidated sedimentary aquifers provide only interstitial habitats within the primary porosity of the clastic sediments. The chemically-deposited aquifers are characterised by secondary porosity with karstic voids in the calcrete and vuggy porosity in the pisolite (Johnson and Wright 2001). Secondary porosity is also developed in the basement rock aquifers in fractured and weathered zones or along bedding plane partings or joints. Across most of the Pilbara region, groundwater salinities are fresh (< 3000 mg L⁻¹ Total Dissolved Solids) but they may be locally saline where evapo-concentration occurs within internal drainage basins such as the Fortescue Marsh (Commander 1989) or even hypersaline on the coastline (Semeniuk 1996). Anchialine habitats are present in coastal areas such as the lower Fortescue River where there is a saltwater interface (Commander 1993). Other groundwater habitats include many springs and spring-brooks, and extensive hyporheic habitats developed in the alluvium of surface watercourses.

Stygofauna

Sampling methods and coverage

As has been the case elsewhere in the world, sampling for stygofauna in the Pilbara has been constrained by the availability of suitable access points to groundwater. Most sampling to date has been undertaken in bores, of which there are > 3,700 (Allen 1997) associated with water supply and mine dewatering operations, and to a lesser extent in geotechnical drill holes, pastoral wells, springs, and the hyporheos. Of 223 sampled sites, 214 (96 %) were bores or wells while spring-brooks and springs (5 sites) and the hyporheos (4 sites), have been comparatively under-sampled. Sampling methods have consisted mostly of hauling a plankton net (250 or 350 µm mesh) through the water column in bores and wells, while springs and shallow hyporheic habitats have been sampled by modified 'kick sampling' (Halse *et al.* 2002), Bou Rouch pumping (Bou & Rouch 1967), or the Karaman-Chapuis method (Camacho 1992a). Sampling has mostly been of low intensity with one sampling method applied and a single sample from each site, although the borefields developed for water supply or mine dewatering have been sampled more than once.

Published records

Of 332 published records, more than one-half (56 %) lie in the Fortescue Basin (186 records), nearly one-third (31 %) in the Ashburton (52) and Onslow Coast (51) Basins, and the remaining 13 % in the De Grey (24) and Port Hedland Basins (19) (Figure 3). There are few published records from the upper catchments of the Ashburton, De Grey, and Port Hedland Basins. The clustered distribution of records reflects the concentration of sampling in aquifers with borefields or wells
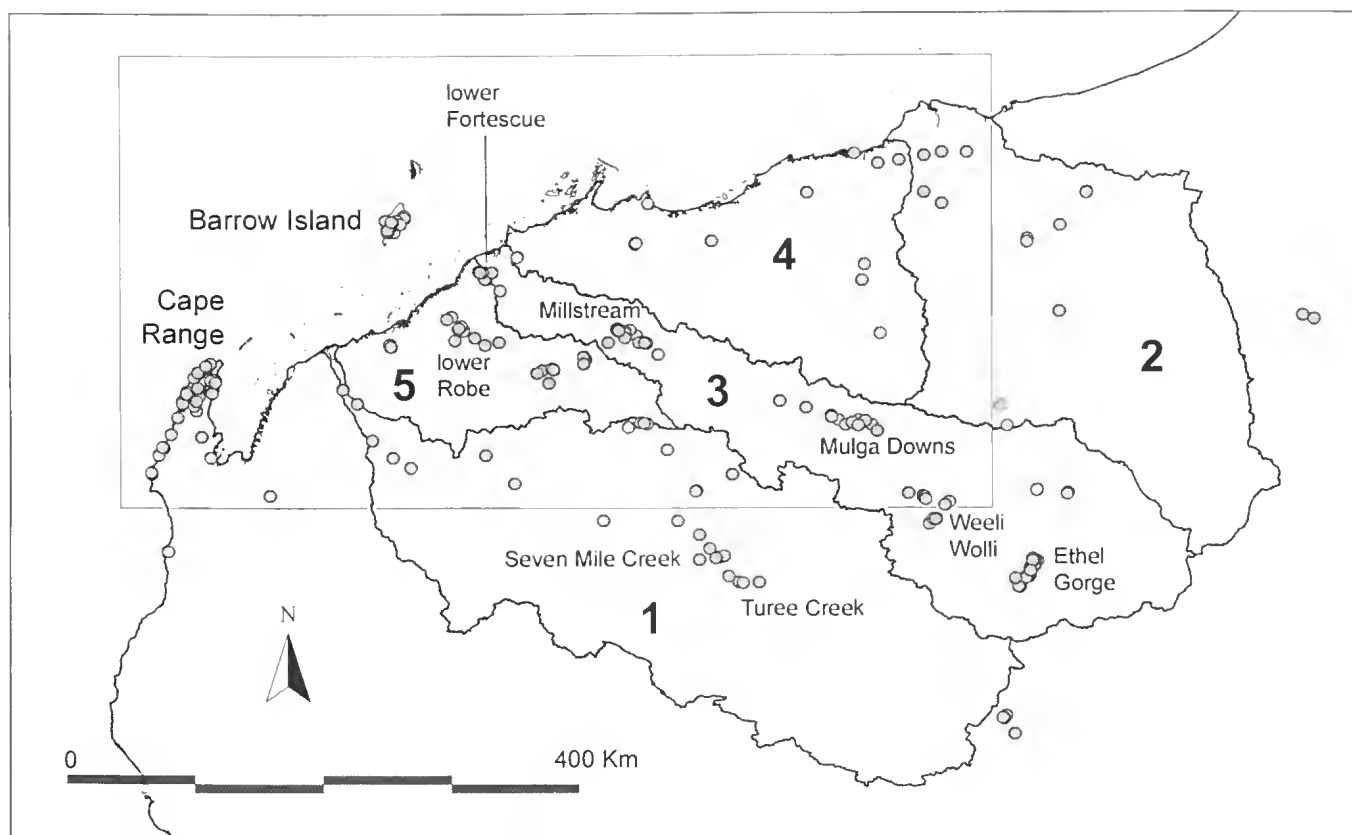
Figure 3. Distribution of published stygofauna records of the Pilbara region and adjacent localities including Cape Range and Barrow Island. Sampled aquifers named in the text are shown, and the five major hydrographic basins (numbered as in Figure 2). Boxed area refers to Figure 5.

developed for water supply or mine dewatering, such as Ethel Gorge (68 records), Millstream (42), lower Robe (38), lower Fortescue (23), Mulga Downs (23), Weeli Wolli (14), Seven Mile Creek (13), and Turee Creek (6). Mulga Downs is the only location where concentrated sampling has occurred in pastoral wells, rather than a water supply or mine dewatering borefield.

Systematics

Published literature records 78 species from the Pilbara belonging to 41 genera and 21 families (Table 1). This compares with 24 species (22 genera) and 25 species (15 genera) found at Cape Range and Barrow Island, respectively. Recorded diversities from Cape Range (63 records, > 30 sites) and Barrow Island (42 records, > 20 sites) are likely to approach actual diversities because considerable sampling and taxonomic effort has been applied to these areas over a number of years. For the size of the area, proportionately less effort has been applied to the Pilbara and the diversity in Table 1 may be a substantial under-estimate. For example, recent collecting suggests much greater diversity of ostracods and bathynellids than previously recognized (I Karanovic, pers. comm.; J-L Cho, pers. comm.).

Knowledge of the Pilbara stygofauna is at an early stage and as further taxonomic work is undertaken the number of species in the Pilbara will likely increase and the proportions of various faunal groups may change. Nonetheless, the synopsis of obligate groundwater species across the world by Botosaneanu (1986), which

recorded approximately 3,574 species belonging to 17 major taxonomic groups, makes a useful point of reference. To date, formally described representatives from only nine of the 17 major faunal groups have been recorded from groundwaters of the Pilbara region (Figure 4), although representatives (mostly undescribed) of six other major groups (Mollusca, Oligochaeta, Polychaeta, Rotifera, Nematoda, Turbellaria) are known to be present (M. Scanlon, J. Cocking, H. Barron, A. Pinder, J. McRae, unpublished data). Nearly three-quarters (73.8 %) of published records are Copepoda, followed by Ostracoda (12.7 %) and then Amphipoda (5.1 %), with all other groups included in the remaining 8.4 %. Groups that have not so far been recorded from the Pilbara are Remipedia and Coleoptera, both of which are present in adjacent regions, respectively at Cape Range (Yager & Humphreys 1996), and in the Gascoyne (Watts and Humphreys 2004) and Little Sandy Desert regions (M. Scanlon, J, Cocking, H. Barron, unpublished data).

Several faunal groups that are poorly represented in the rest of the world appear to be relatively species-rich in the Pilbara: for example, the region supports two of the four known species of Spelaeogriphacea (Poore and Humphreys 2003). The Pilbara fauna also appears to be disproportionately rich in Ostracoda (27 % of Pilbara fauna cf. 3 % World) and Copepoda, (39 % cf. 17 %). The large number of species belonging to these two groups (Ostracoda: 18 species in eight genera; Copepoda: 31 species in 18 genera) partly reflects the focus of taxonomic effort but, nonetheless, the groups are clearly

Table 1

Systematic list of genera with the number of described stygal species in the Pilbara region, Cape Range and Barrow Island, and a cross reference number to the literature source. *But see Finston *et al.* (2004) for molecular evidence that many of the species of *Chydaekata* are synonyms.

Higher Rank	Family	Genus	Pilbara	Cape Range	Barrow Island	Source
Acarina	Momonidae	*Hesperomomonia*	1			12
	Mideopsidae	*Tiramideopsis*	1			12
Polychaeta	Spionidae	*Prionospio*		1		35
	Syllidae	*Sphaerosyllis*		1		35
		Typosillis (Ehlersia)		1		35
Amphipoda	Bogidiellidae	*Bogidomma*			1	2
	Hadziidae	*Hadzia*		1	1	3, 39
	Melitidae	*Nedsia*		1	10	1, 2, 5, 15
		Norcapensis		1		4
	Paramelitidae	*Chydaekata*	15			5, 10
		Molina	1			5
		Pilbarus	1			4
Bathynellacea	Parabathynellidae	*Atopobathynella*			1	14
Copepoda	Ameiridae	'Genus A'	2			38
		'Genus B'	1			38
		'Genus C'			1	38
		Inermipes			1	8
		Nitokra		1	1	24
		Stygonitocrella	3			38
		Parapseudoleptomesochra	1			38
	Canthocamptidae	*Elaphoidella*	1			38
	Cyclopidae	*Allocyclops*			1	21
		Apocyclops	1	1		29, 38
		Diacyclops	6	1	1	28, 38
		Halicyclops	2	2	2	26, 30, 38
		Fierscyclops	2			38
		Mesocyclops	2			16, 29, 38
		Metacyclops	2	1		22, 26, 29
		Microcyclops	1	1		26, 29
		'Genus D'	1			38
		Thermocyclops	1			38
		Tropocyclops	1			38
	Diosaccidae	*Schizopera*	2			38
	Ectinosomatidae	*Pseudectinosoma*	1			38
	Epacteriscidae	*Bunderia*		1		16
	Parastenocaridae	*Parastenocaris*	1			38
	Pseudocyclopiidae	*Stygocyclopia*		1		17
	Speleophriidae	*Speleophria*		1		17
	Tetragonicipitidae	*Phyllopodopsyllus*		1	1	23
Decapoda	Atyidae	*Stygiocaris*	1	2	1	13, 15
Isopoda	Amphisopididae	*Pilbaraphreatoicus*	1			25
	Cirolanidae	*Haptolana*	1	1	1	7, 15, 34
	Tainisopidae	*Pygolabis*	1			36
Ostracoda	Candonidae	*Areacandona*	2			20
		Deminutiocandona	1			18
		Humphreyscandona	6			19
		Meridiescandona	2			18
		Neocandona	1			20
		Notacandona	2			19
		Origocandona	2			20
		Pilbaracandona	2			19
	Darwinulidae	*Vestalenula*	2			11, 27
	Limnocytheridae	*Limnocythere*	1			11
	Thaumatocyprididae	*Danielopolina*		1		9
Spelaeogriphacea	Spelaeogriphidae	*Mangkurtu*	2			32, 33
Remipedia	Speleonectidae	*Lasionectes*		1		37
Thermosbaenacea	Halosbaenidae	*Halosbaena*	1	1	1	15, 31, 34
Pisces	Eleotridae	*Milyeringa*		1	1	13
	Synbranchidae	*Ophisternon*		1		14
		No. described species	78	24	25	
		No. described genera	41	22	15	
		No. Families	21	16	11	

Table 1 sources: 1 (Barnard & Williams 1995), 2 (Bradbury & Williams 1996a), 3 (Bradbury & Williams 1996b), 4 (Bradbury & Williams 1997), 5 (Bradbury 2000), 6 (Bradbury 2002), 7 (Bruce and Humphreys 1993), 8 (Lee and Huys 2002), 9 (Danielopol *et al.* 2000a), 10 (Finston *et al.* 2004), 11 (Halse *et al.* 2002), 12 (Harvey 1998), 13 (Humphreys & Adams 1991), 14 (Humphreys 1999b), 15 (Humphreys 2001b), 16 (Jaume & Humphreys 2001), 17 (Jaume *et al.* 2001), 18 (Karanovic I. 2003b), 19 (Karanovic & Marmonier 2003), 20 (Karanovic I. 2005), 21 (Karanovic T. 2003), 22 (Karanovic 2004a), 23 (Karanovic *et al.* 2001), 24 (Karanovic & Pesce 2002), 25 (Knott & Halse 1999), 26 (Laurentiis *et al.* 1999), 27 (Martens & Rossetti 2002), 28 (Pesce & Laurentiis 1996), 29 (Pesce *et al.* 1996a), 30 (Pesce *et al.* 1996b), 31 (Poore & Humphreys 1992), 32 (Poore & Humphreys 1998), 33 (Poore & Humphreys 2003), 34 (Humphreys 2000a), 35 (Wilson & Humphreys 2001), 36 (Wilson 2003), 37 (Yager & Humphreys 1996), 38 (Karanovic 2006 in press), 39 (Sawicki *et al.* 2004).
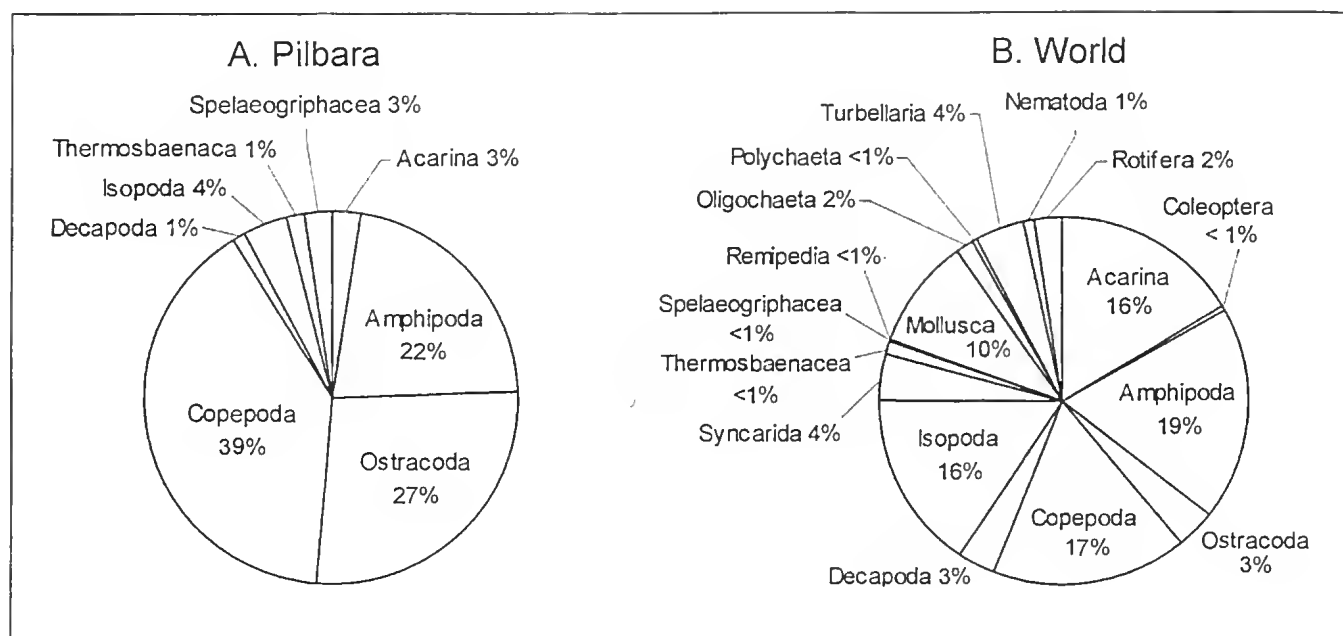
A. Pilbara

Spelaeographacea 3%

Thermosbaenaca 1%

Isopoda 4%

Decapoda 1%

Acarina 3%

Amphipoda 22%

Copepoda 39%

Ostracoda 27%

B. World

Turbellaria 4%

Nematoda 1%

Polychaeta <1%

Oligochaeta 2%

Remipedia <1%

Spelaeographacea <1%

Thermosbaenacea <1%

Syncarida 4%

Rotifera 2%

Coleoptera < 1%

Acarina 16%

Mollusca 10%

Amphipoda 19%

Isopoda 16%

Copepoda 17%

Decapoda 3%

Ostracoda 3%

Figure 4. Systematic composition of described stygofauna from the Pilbara region (A) compared with World Average (B) derived primarily from Botosaneanu (1986) as in Scarsbrook *et al.* (1998) and supplemented with data in Boutin (1998).

speciose in groundwaters of the Pilbara region. Copepoda are also speciose in the Murchison (31 species in 16 genera) (Karanovic 2004b) and Cape Range (11 species, 10 genera) (Table 1) whereas Ostracoda are less diverse in adjacent regions (Murchison: five species, one genus; Cape Range: one species).

A striking feature of the groundwater fauna in north-west Western Australia is the high proportion of species with marine Tethyan, Pangean and/or Gondwanan affinities (Humphreys 1993a, 2000b, Knott 1993). Most of the marine faunal elements recorded in the Pilbara region (atyid decapods, cirolanid isopods, thermosbaenaceans, melitid amphipods, and the cyclopid copepods *Halicyclops* and *Apocyclops*) are shared at generic or supra-generic level with nearby Cape Range and Barrow Island. As noted by Humphreys (2001a), the marine elements appear to share a generalised distribution coinciding with the present coastal margins of the Northern Carnarvon Basin and the Pilbara Craton, with the greatest inland penetration (110 km, 300 m asl) by Thermosbaenacea in the Robe River valley (Figure 5).
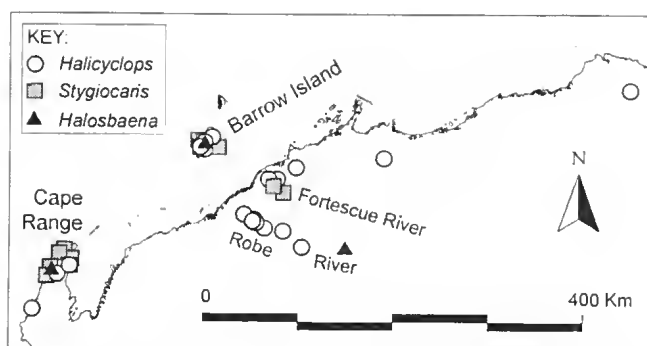

KEY:
○ *Halicyclops*
□ *Stygiocaris*
▲ *Halosbaena*

Barrow Island

Cape Range

Fortescue River

Robe River

N

0   400 Km

Figure 5. Distribution of some marine and/or Tethyan elements shared between the Pilbara region, Cape Range and Barrow Island: *Halicyclops* (Cyclopidae), *Stygiocaris* (Atyidae), *Halsobaena* (Thermosbaenacea). Refer Figure 3 for area shown.

The Pilbara region differs from Cape Range and Barrow Island in the occurrence of several ancient freshwater lineages including paramelitid amphipods, tainisopid and phreatoicid isopods, momonid and mideopsid acarines, various copepod taxa, and ostracods: (Candonidae, Darwinulidae, Limnocytheridae), all of which appear to be absent from the younger Tertiary karst areas. To date, the only stygal freshwater known from the Tertiary karsts is an undescribed species of phreodrilid oligochaete from Barrow Island (A. Pinder, pers. comm.); other phreodrilids (mostly undescribed) are recorded from groundwaters in the Pilbara and Murchison regions (Pinder 2001). Sixteen freshwater genera (59 % of total Pilbara genera) have to date been recorded only in the Pilbara region, including *Mangkurtu* (Spelaeogriphacea), *Pilbarophreatoicus* (Phreatoicidea), *Pygolabis* (Tainisopidae), *Molina*, *Pilbarus* and *Chydaekata* (Parameletidae), 'Genus A', 'Genus B', (Ameiridae), 'Genus C' (Cyclopidae), and the eight genera of candonine ostracods (Table 1). While taxonomic knowledge of the Murchison and other adjacent regions is still incomplete, some distinct differences from the Pilbara region have already been noted (Humphreys 2001a). For example, both *Haloniscus* isopods (Taiti and Humphreys 2001) and dytiscid beetles (Watts and Humphreys 2004) seem to be absent from the Pilbara.

The richness of species recorded from individual aquifers in the Pilbara region appears roughly proportional to sampling effort: Ethel Gorge (31 species: 43 sites), Millstream (16: 24), Mulga Downs (11: 10), lower Fortescue (10: 10), lower Robe (9: 8), Weeli Wolli (7: 6), Seven Mile Creek (5: 7), Turee Creek (4: 5). The three aquifers with more than 10 species contain karstic calcrete and dolomite and the two richest aquifers contain comparatively high diversity, respectively, of paramelitid amphipods and candonine ostracods (15 species and 5 species, Ethel Gorge), and cyclopid copepods of the genus *Diacyclops* (5 species, Millstream).

Discussion

Sampling coverage of the Pilbara region is skewed, in terms of both areal coverage (Figure 3) and the different types of groundwater habitats represented. This is partly a consequence of logistical constraints that have directed much of the sampling towards water supply borefields and mine dewatering sites, where access is afforded to many bores within a small area, although widely dispersed pastoral wells have also been sampled. However, even if the available bores had been randomly sampled, sampling would have been biased because bores and wells are concentrated in high-yield aquifers (mostly Cainozoic valleyfill sediments with calcrete and limonite, or Proterozoic carbonates). There are comparatively few bores or wells in low-yielding aquifers but meiofauna have been recorded from fractured igneous and sedimentary (ore-bearing) rocks (Eberhard 1998; Eberhard & Humphreys 1999). Sampling of springs, or the benthic and interstitial zones of spring-brooks and rivers has been too limited to draw general conclusions about the degree of faunal overlap and importance of groundwater-surface water ecotones but these habitats have also yielded stygofauna (e.g., Poore & Humphreys 1998; Halse *et al*. 2002). Caves provided important access points for sampling stygofauna at Barrow Island and Cape Range, but in the Pilbara region only a handful of enterable caves are known at three locations (Millstream, Rippon Hills and Tongolola Creek) (Western Australian Speleological Group, pers. comm.). Nonetheless, the Pilbara region contains extensive karstic carbonates and we predict that karst springs will have rich stygobite faunas.

In evaluating the biodiversity of a region, comparisons are often made with endemism and species richness of other areas (*e.g.*, Storey *et al*. 1993; Horwitz 1997; Halse *et al*. 2000; Halse 2004; Pinder 2004). However, endemism is scale-dependent (*e.g.*, local endemism versus regional endemism) and assessment assumes a complete knowledge of species taxonomy and distribution. For most Pilbara taxa this knowledge is very incomplete. While many species appear to have localised distributions, recent sampling has shown some taxa are more widely distributed than published records suggest (J. Reeves, M. Scanlon, J. Cocking and H. Barron, unpublished data) and a molecular genetic study of amphipods by Finston and Johnson (2004) in the Fortescue and Ashburton River basins found evidence of genetic exchange within sub-catchments. Hence, we remain cautious in interpretation of local endemism patterns at this time. However in terms of regional endemism, the Pilbara region contains several major freshwater lineages (phreatoicid isopods, momonid and mideopsid acarines) that have not been recorded at Cape Range, Barrow Island or in the Murchison. Independently of endemism, the Pilbara region has comprehensive systematic diversity, with nearly all major stygofauna groups represented by published or unpublished records, including several higher-level systematic lineages that are phylogenetic relics (see Humphreys 2001a).

Valid comparison of species richness between regions is hindered because of differences in area, habitats, seasonality, taxonomic resolution, sampling methods and effort (*e.g.*, Horwitz 1997). Most assessments of subterranean biodiversity focus on the comparative richness of stygobites because these species are permanently confined to subterranean habitats (see for example Knott 1993; Culver & Sket 2000; Humphreys 2000b). In groundwater environments that are more or less isolated from surface waters, such as occur at Cape Range, Barrow Island and in most of the Pilbara region, the stygofauna consists almost entirely of stygobites. In a review of world hotspots of subterranean biodiversity, which specifically excluded porous aquifers and interstitial species, Culver and Sket (2000) listed 20 individual caves, springs and karst wells that contained 20 or more stygobites and/or troglobites (obligate terrestrial subterranean species). The one Australian hotspot (Bayliss Cave in Queensland) included in the list supported exclusively troglobites, while Cabaret Cave at Yanchep near Perth (Figure 1), which contained > 40 aquatic species (Jasinska *et al*. 1996; Jasinska & Knott 2000), was not included because the majority of species are not strictly stygobitic (Culver and Sket 2000).

Outside of the Pilbara region, the highest published diversity of stygobites from an individual karst aquifer in Australia is 25 species from Barrow Island (Table 1, and Humphreys 2000b). Ignoring Ethel Gorge, where there is molecular evidence that many of the species of *Chydaekata* are not valid (Finston *et al*. 2004), the richest aquifer in the Pilbara region is Millstream with 16 species. The next richest location (12 species) is a calcrete aquifer (Lake Violet) in the Murchison (Watts and Humphreys 2003). Comparisons with eastern Australia are difficult, because of poor taxonomic resolution within most groups and limited sampling coverage of meiofauna, but the richest single karst area assemblages in the east appear to support ≤ 10 stygobites (Eberhard *et al*. 1991; Eberhard 1992, 1993; Eberhard & Spate 1995).

While most studies have focussed on stygobites in karst aquifers because of the speleological basis of much subterranean work (e.g., Camacho 1992b), stygobites occur more widely in alluvial aquifers (see for example Dole-Olivier *et al*. 1994; Stanford *et al*. 1994; Ward & Voelz 1994; Danielopol *et al*. 2000b; Marmonier *et al*. 2000). Alluvial aquifers in the Rhone River Basin, France, hold greater stygobite richness than adjacent karst aquifers within the same drainage basin (Dole-Olivier *et al*. 1994). This situation appears to be mirrored in the Pilbara region where recent sampling using pump methods indicates that some alluvial aquifers in the lower Robe and lower Fortescue Rivers have very high richness, including > 20 stygobites collected from a single bore (M. Scanlon and J. Cocking, unpublished data). This richness exceeds that recorded from any single bore, well or cave in Australia, the previous richest site was Bundera Sinkhole at Cape Range with 12 species (Humphreys 1999a).

With the exception of large taxa such as fish, which are rare in Australian subterranean waters and worldwide tend to be restricted to karst (Proudlove 1997; Humphreys 1999b), stygofaunal elements from the Pilbara region and adjacent areas tend to colonise most groundwater environments, whether karst conduit or the benthic and interstitial zones of springs and spring-brooks. This applies to both meiofauna (copepods) and meso/macrofauna (amphipods, isopods, decapods). Taxa originally identified from karstic habitats at Cape Range

and Barrow Island (*Stygiocaris, Nedsia, Halosbaena, Haptolana, Halicyclops, Apocyclops*) were subsequently collected in alluvial river-aquifer systems on the Pilbara coastal plain (Humphreys 2001a). Humphreys (1993ab) suggested that the Cape Range and Barrow Island karsts were colonised by fauna which migrated either from the Pilbara Craton or the fringing Mesozoic deposits. Hence future sampling of Pilbara coastal margins and islands (*e.g.*, Dampier Archipelago, Montebello Islands), particularly in anchialine habitats, may reveal the presence of other marine Tethyan and/or anchialine elements. Irrespective of future discoveries, this review confirms that within the already world-recognised subterranean fauna richness of north-west Western Australia, the Pilbara region is important for the conservation of subterranean biodiversity.

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Fossil foraminiferal assemblages from Pleistocene seagrass-bank deposits of the southern Perth Basin, Western Australia, and their palaeotemperature implications

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Abstract

Fossil foraminifera were collected from three Pleistocene seagrass-bank deposits in the laterally contiguous Tims Thicket Limestone, Myalup Sand, and Kooallup Limestone in the southern Perth Basin, Western Australia. In total, 112 species of foraminifera were recorded. Tims Thicket Limestone and Kooallup Limestone had diverse assemblages (> 90 species) characterised by a *Marginopora-Amphisorus-Cibicides* assemblage. The limestone lens in the quartz-rich Myalup Sand had a moderately diverse assemblage (35 species) and was characterised by a *Lamellodiscorbis-Rotorboides* assemblage. Comparisons of the fossil assemblages with modern ecological assemblages from seagrass communities from a range of warm to cool climate settings along the Western Australian coast indicate that the limestone and siliciclastic formations formed in warm and cool water settings, respectively. Hence, these formations preserve a warm-cool-warm cycle of carbonate deposition in the late Quaternary, most likely linked to latitudinal shift in climate zones compounded by changing strength of the Leeuwin Current.

Keywords: Pleistocene foramininfera, seagrass facies, Perth Basin, Pleistocene limestone, sea temperatures

Introduction

In Western Australia, seagrass banks contributed to the formation of abundant carbonate deposits along the coast from the Neogene to Quaternary, as a result of prolonged sedimentation in a passive-margin tectonic setting (Davies 1970; Searle & Semeniuk 1985; Semeniuk & Searle 1985; Semeniuk *et al.* 1988). In the Perth Basin, both local modern and Pleistocene seagrass-bank material is available for study. This material is ideal for palaeoecological reconstruction based on foraminiferal assemblages due to its species richness and the continuity of Pleistocene species up to the present. Modern ecological analogues based on living foraminiferal assemblages for different climate settings are described for the Western Australian coast in T A Semeniuk (2000, 2001). These assemblages provide a baseline for the palaeoecological interpretation of Pleistocene material in this study. Semeniuk (1996) provides a detailed stratigraphic framework for the three Pleistocene formations.

Neontology incorporates both living assemblages (biocoenoses) and death assemblages (thanatocoenoses). Traditionally, fossil assemblages in palaeoecology are compared with death assemblages within modern (neontological) assemblages, since death assemblages are viewed as a long-term 'average' accumulations of the living assemblages. It is these death assemblages also that are most likely to be preserved in the stratigraphic column. However, in this study, Pleistocene assemblages are compared with living epiphytic assemblages of foraminifera, *i.e.,* those foraminiferal assemblages that are living on seagrass leaves in the modern environment. There are several reasons for this. Firstly, living epiphytic populations do not show the heterogeneity related to spatial variation in microhabitat that is typical for benthic populations of foraminifera, and thus, they can be easily used to characterise a specific habitat at the local scale (T A Semeniuk 2000). Secondly, epiphytic populations of foraminifera appear to closely reflect local ambient environmental conditions such as water chemistry, temperature and related epiflora at the time of sample collection, and thus are more reliable environmental and temperature indicators than benthic species (T A Semeniuk 2001). Thirdly, death assemblages represent a mix of epiphytic and benthic species of foraminifera accumulated over an unknown time interval. In addition, death assemblages typically contain reworked material, especially in the nearshore environments of southwestern Australia, where reworking of local onshore deposits is typical. As such, the death assemblages can reflect integrated population dynamics of different species, integrated assemblages from different local environmental conditions over time, effects of sedimentary processes on sediment composition, including preferential preservation and sorting of foraminiferal tests, as well as a minor contribution from reworked Holocene or older material derived from onshore deposits. Thus, in the nearshore environment, living foraminiferal assemblages can be used to clarify which components of a neontological assemblage are related to a given set of environmental conditions, which components result from long-term accumulation or reworked material.
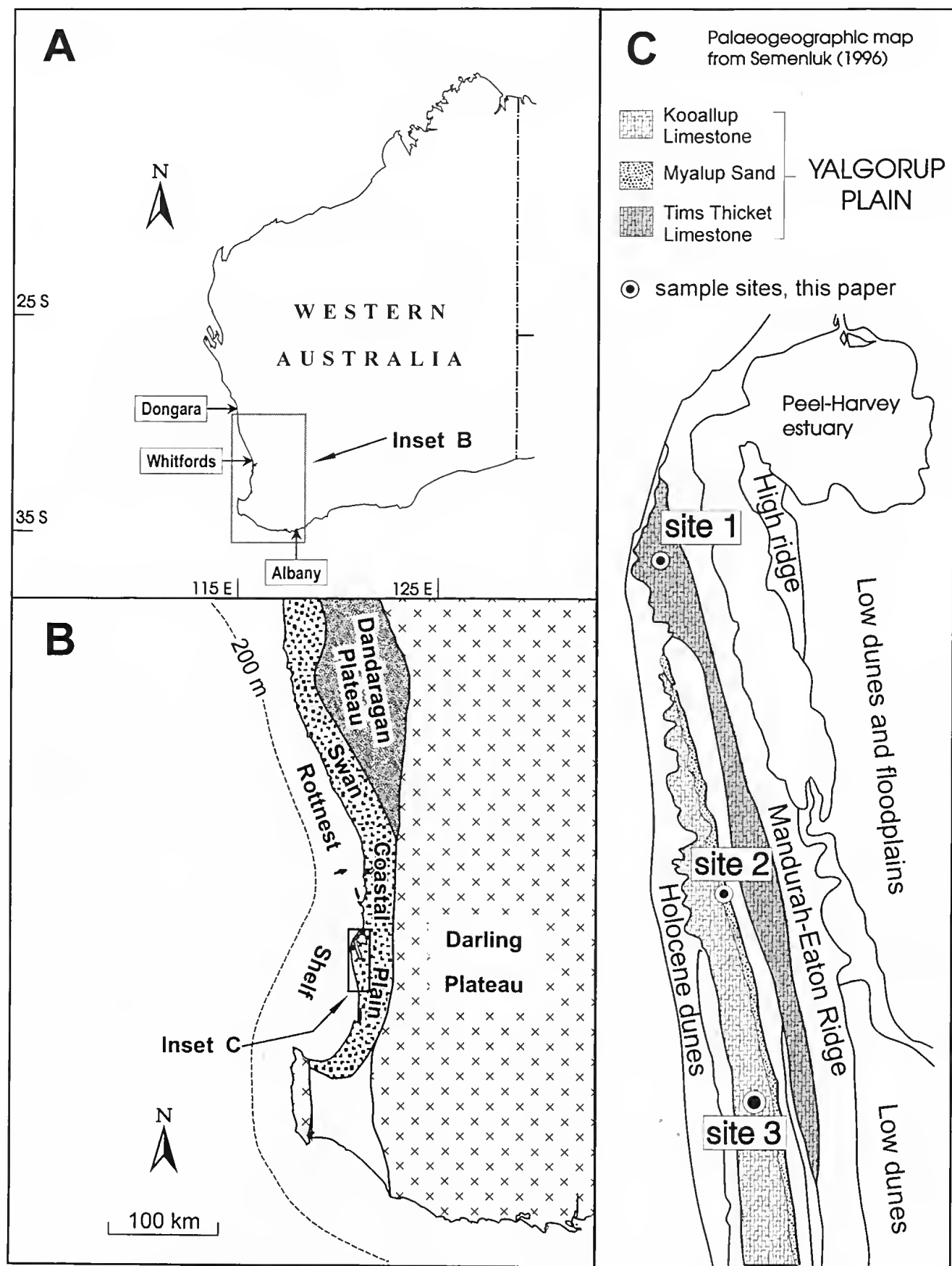
Figure 1. A. Location map, and location of sampling sites (Dongara, Whitfords, Albany) of T A Semeniuk (2000) for living assemblages of foraminifera. B. The Swan Coastal Plain (McArthur & Bettenay 1960), and location of detailed study area of the Yalgorup Plain (inset C). C. Outcrop of the Tims Thicket Limestone, Myalup Sand and Kooallup Limestone formations on the Yalgorup Plain, and location of the sampling sites, this paper, at quarry sites in the Tims Thicket Limestone (site 1) and the Kooallup Limestone (site 3), and the location of the transect through Myalup Sand (site 2) as shown in Figure 2.

The living assemblages described in earlier papers by T A Semeniuk (2000, 2001) are used in this study to decipher environmental or climate signals in the fossil thanatocoenoses on the basis of indicator species or taxonomic groups determined from modern analogues in different climate settings. Comparison of modern and Pleistocene material provides estimates of palaeo sea temperatures for each Pleistocene formation, as well as insights into carbonate productivity and climate change during the late Quaternary.

Stratigraphic and palaeogeographic setting

The nearshore-marine carbonate deposits which formed along the coast of Western Australia during the interglacial periods of the late Pleistocene to Holocene include units derived from seagrass and marginal seagrass environments (Semeniuk & Johnson, 1982; Semeniuk 1996). One of the best-developed and laterally extensive deposits, comprising seagrass-bank, beach and dune sequences underlies the Yalgorup Plain of the southern Swan Coastal Plain in the Perth Basin (McArthur & Bettenay 1960; Semeniuk 1996). Here, seagrass-bank units occur in three contiguous Pleistocene formations (Fig. 1).

The Pleistocene coastal limestones in this region were originally referred to by previous workers as Coastal Limestone, then as Tamala Limestone (Playford *et al.* 1976). However, on the basis of lithology, stratigraphy and geological history, Semeniuk (1995) assigned the sedimentary carbonate and quartz sand deposits in this area to the Tims Thicket Limestone, Myalup Sand and Kooallup Limestone. The three formations are shore-parallel and are separated by unconformities, suggesting that there were at least three separate marine transgressions during the late Pleistocene (Fig. 1). Semeniuk (1996) identified units within the marine portion of the sequences as seagrass-bank deposits based on their position within the shoaling stratigraphic sequence, their microstratigraphic and sedimentological features, and their fossil molluscan fauna.

Based on their stratigraphy, Semeniuk (1996) reconstructed the palaeogeography and palaeoenvironments of the three Pleistocene formations and showed that they formed as cuspate forelands, barrier or ribbon shoreline deposits at different sealevel stands (Table 1). The formations have very different carbonate content, suggesting differences in carbonate productivity linked to changes in palaeogeographic or climate setting.

Methods

Field techniques

Data on epiphytic foraminifera from modern seagrass meadows form the basis of the information on the living foraminiferal assemblages used in this paper. In the modern environments, T A Semeniuk (2000) sampled epiphytic foraminifera in seagrass meadows in 1.0–1.5 m depth of water in three climatically distinct areas (Fig. 1), *i.e.*, at Dongara, a warm water environment, at Whitfords, an intermediate climate setting, and at Albany, a relatively cool water environment. Within each geographic/climate setting, nine 9-cm diameter cores (three cores within 1m² separated by at least 25 m from the next set of three cores) were used to harvest seagrass leaves and their foraminiferal epiphytes. The results of the study into living foraminiferal assemblages are presented in T A Semeniuk (2000, 2001), and will not be re-iterated here other than for comparative purposes.

Samples of weakly cemented Pleistocene limestone containing foraminifera were collected from the Tims Thicket Limestone and Kooallup Limestone from vertical exposures in quarry sites within the Yalgorup Plain (Fig. 1). The Tims Thicket Limestone sampling site (site 1, this paper) is a quarry at 32° 39' 09.52" 115° 37' 18.85" located at site 5 transect 1 of Semeniuk (1995). The limestone lens in the Myalup Sand (site 2, this paper) was intersected in a core at 32° 54' 51.19" 115° 42' 11.08" located at site 6 transect 2 of Semeniuk (1995). The Kooallup Limestone sampling site (site 3, this paper) is a quarry at 32° 01' 23.71" 115° 42' 27.55" located at site 2 transect 4 of Semeniuk (1995).

In the quarries cut into the Tims Thicket Limestone and the Kooallup Limestone, material was sampled from a horizon about 10–20 cm thick within the seagrass facies, located 1 m below trough-bedded low-tidal to shallow-water beach facies of Semeniuk (1996), and 0.5 m below the upper seagrass-unit boundary (Fig. 2). In modern environments, this stratigraphic interval is equivalent to sediments from 1.0–1.5 m of water, *i.e.*, the depth at which collections of modern living foraminiferal material took place (T A Semeniuk, 2000), as described above, *i.e.*, the sampling interval in the Pleistocene limestone was the facies-equivalent of the sampling sites in the modern environments. The thickness of the beach facies in the Pleistocene deposits is similar to that in Holocene sequences (Semeniuk 1996; Semeniuk & Johnson 1982), suggesting that the tidal range was microtidal during the deposition of the Pleistocene units.

Table 1

Summary of palaeogeographic setting, stratigraphy, Pleistocene sealevel position, and lithologic signature of the three contiguous Pleistocene formations of the Yalgorup Plain (after Semeniuk 1996)

Formation	Palaeogeographic setting	Simplified stratigraphic setting	Pleistocene sealevel position	Carbonate content
Tims Thicket Limestone	cuspate foreland	shoaling sequence of seagrass bank to dune facies	+ 3 m above present MSL	high
Myalup Sand	shoreline ribbon	limestone lenses with a coastal quartz sand formation	- 2–3 m below present MSL	low
Kooallup Limestone	cuspate foreland	shoaling sequence of seagrass bank to dune facies	+ 3–4 m above present MSL	high
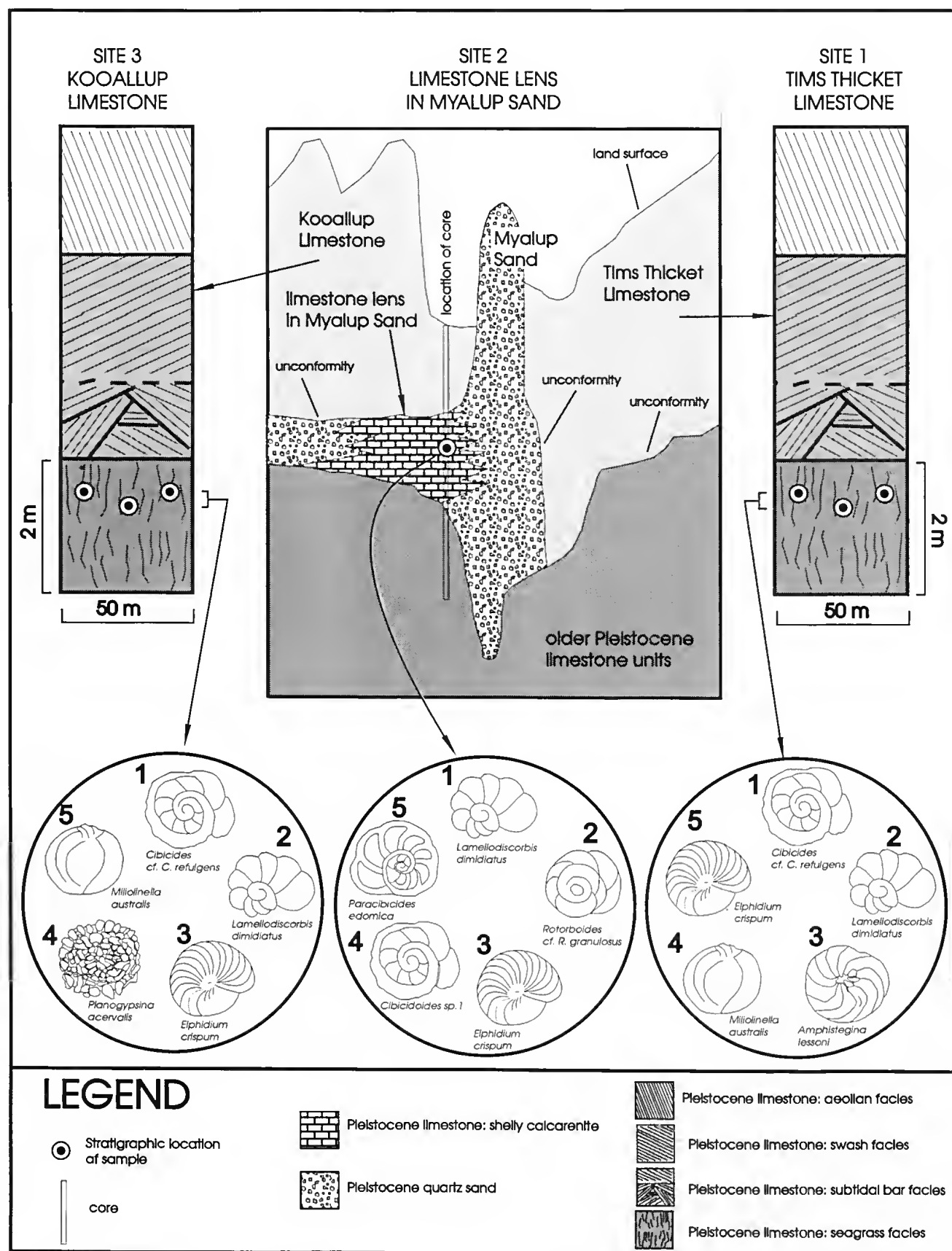
Figure 2. Stratigraphic setting of samples for the three Pleistocene formations: detailed stratigraphy from quarry sections, showing location of samples for the Tims Thicket Limestone at site 1 and Kooallup Limestone at site 3, and location of drill core and sample for the localised limestone lens in the Myalup Sand at site 2. The five most abundant foraminifera from each Pleistocene formation are diagrammatically shown in order of abundance; Tims Thicket Limestone – 1. *C.* cf. *refulgens*, 2. *L. dimidiatus*, 3. *A. lessoni*, 4. *M. australis*, and 5. *E. crispum*; Myalup Sand – 1. *L. dimidiatus*, 2. *R.* cf. *granulosus*, 3. *E. crispum*, 4. *Cibicidoides* sp. 1, and 5. *P. edomica*; Kooallup Limestone: 1 – *C.* cf. *refulgens*, 2. *L. dimidiatus*, 3. *E. crispum*, 4. *P. acervalis*, 5. *M. australis*.

For the Tims Thicket Limestone and Kooallup Limestone, three replicate samples of Pleistocene limestone were collected in close mutual proximity (within 50 m of each other; Fig. 2). The samples were collected in replicate to assess lateral variation in composition within a formation and to determine the statistical significance of composition differences between formations. Samples consisted of about 250 ml of friable material collected 5 cm below the weathered vertical surface in the quarry section.

The limestone lenses in the Myalup Sand do not crop out, but one carbonate-rich sample (100 ml in volume) was obtained from a drill-core. The location of the drill hole in the Myalup Sand relative to the local stratigraphy is shown in Figure 2.

Laboratory techniques

Standard palaeontological methods, outlined in Haynes (1981), were followed in this study. Pleistocene samples were soaked in water to disaggregate sediment as much as possible. Material was wet sieved through a 63-μm mesh and oven dried. The vast majority of material was very weakly cemented or uncemented, and so it disaggregated readily and fully. At least 300 specimens were picked from sediment scattered on a picking tray. The volume of sediment picked was recorded to calculate the approximate number of foraminifera occurring in one cubic centimeter of sediment. Specimens were sorted on taxonomic slides and identified using standard reference material (Ellis & Messina 1940 *et seq.*) and taxonomic literature relevant for the Western Australian region including Jones (1994), Loeblich & Tappan (1988, 1994), and Parr (1932a, 1932b, 1945). Assemblage data on the number of individual specimens of each species were compiled for each sample (Appendix 1).

Quantitative data analyses

Density and diversity of foraminiferal assemblages were calculated using standard ecological measures. The total foraminiferal density was calculated from three replicates for each formation, whereas diversity was calculated for each sample and a mean diversity was calculated for each formation. The Fisher index (Fisher *et al.* 1943; Fisher & Yates 1953) was used to categorise species heterogeneity while the Shannon index (Pielou 1975) was used to determine evenness of the assemblages from each formation.

Analysis of variance was carried out on the species abundance for the Tims Thicket Limestone and Kooallup Limestone (statistical analysis was only possible for formations with replicate samples) to identify important differences between formations. A significant F-ratio is obtained for species that showed greater variation between formations than within replicates from a given formation. Non-significant F-ratios imply that the lateral variation within a formation is of sufficient magnitude to obscure differences between formations, in which case the hypothesis that all samples characterise an identical assemblage cannot be rejected at the 95% confidence level. The criterion used to choose species for statistical analysis was a mean sample count of greater than three specimens. Seventeen of the total 112 species met this criterion.

Palaeoecological reconstructions

Modern assemblages of foraminifera, described and illustrated in detail in T A Semeniuk (2000, 2001) form the basis of comparison and palaeo-environmental interpretation of Pleistocene foraminiferal assemblages of this paper. Assemblages are from semi-arid to sub-humid subtropical climate settings, wherein annual sea temperatures range from 20–25 °C at the warmest site and 16–20°C at the coolest site (Pearce *et al.* 1999; T A Semeniuk 2000), Characteristics of the live epiphytic assemblages from these modern sites are:

1. they are all hyaline dominant assemblages

2. moderately diverse assemblages with high evenness characterise the warmest site; the dominant species are *Quinqueloculina* cf. *Q. incisa*, *Vertebralina striata*, *Peneroplis planatus*, *Amphisorus hemiprichii* and *Marginopora vertebralis*.

3. the coolest site has low diversity and moderate evenness and is characterised by the species *Lamellodiscorbis dimidiatus*, *Annulopatellina annularis* and *Rosalina* spp.

Using information on the distribution of living foraminiferal species in modern environments in relation to sea temperatures, criteria to interpret former sea temperatures for Pleistocene environments were developed. The criteria were based on modern taxa, whose abundance and distribution patterns most likely reflect sea temperature (T A Semeniuk 2001). In principle, these criteria would provide a basis for interpreting sea-temperature differences between Pleistocene formations, although in the fossil record this effect cannot be completely decoupled from other abiotic and biotic factors.

Initially, a number of criteria deriving from the modern assemblages were considered for use in reconstructing palaeo sea temperature settings of Pleistocene seagrass-bank environments. These included compositional attributes of the living assemblages at Order, Family, Genus and species level that had strong positive correlation with climate setting, including the number of rotallid, buliminid and miliolid taxa, the number of larger foraminifera, the number of *Quinqueloculina* species, abundance of select species such as *V. striata*, *Q.* cf. *Q. incisa*, *Sorites variabilis* and *Bolivina subreticulata*. In this study, however, the number of larger foraminifera, the numbers of rotallid and miliolid taxa, as well as the abundance of select species such as *S. variabilis*, are used as indicators to interpret former sea temperatures.

Using the information from modern environments as a tool, the composition of fossil foraminiferal assemblages from each of the three formations were compared with modern living epiphytic foraminiferal assemblages, and their former sea temperature settings were interpreted.

Results

General composition of fossil assemblages

A total of 112 species was recorded in fossil foraminiferal assemblages from the seagrass-bank units of the Pleistocene formations (Table 2). Species counts for

Table 2

Complete list of species of Pleistocene foraminifera collected from the Tims Thicket Limestone, Myalup Sand and the Kooallup Limestone.

Order	Taxa	Order	Taxa
Textularia		Rotaliina	
	Gaudryina sp 1	(spirillinids	*Patellina corrugata*
	Textularia pseudogramen		*Planispirillina spinigera*
	Textularia cf. T. sagittula		*Spirillina limbata*
	Textularia sp 1		*Spirillina sp. 1*
Miliolina		(lagenids)	*Fissurina bradyformata*
	Amphisorus hemiprichii		*Sigmoidella elegantissma*
	Biloculinella sp. 1	(buliminids)	*Bolivina sp. 1*
	Cornuspira involvens		*Bolivina sp. 2*
	Cornuspira sp. 1		*Bolivina quadrilatera*
	Cornuspira acicularis		*Buliminoides williamsonianus*
	Marginopora vertebralis		*Fijiella simplex*
	Miliolinella australis		*Loxostoma cf. L. digitale*
	Miliolinella labiosa		*Loxostomina costulatum*
	Miliolinella sp. 1		*Loxostomina limbata*
	Nubecularia luciuga		*Pavonina flabelliformis*
	Parrina bradyi		*Reussella armata*
	Peneroplis pertusus		*Reussella simplex*
	Peneroplis planatus		*Saidovina sp. 1*
	Pseudomassilina australis		*Sigmavirgulina tortuosa*
	Pseudomassilina subgranulata		*Trifarina sp. 1*
	Pyrgo sarsi	(rotallids)	*Acervulina mahabeti*
	Quinqueloculina baragwanathi		*Amphistegina lessoni*
	Quinqueloculina carinata		*Angulodiscorbis quadrangularis*
	Quinqueloculina cf. Q. bicarinata		*Annulopatelinella annularis*
	Quinqueloculina sulcata		*Anomalinoides globosus*
	Quinqueloculina cf. Q. incisa		*Anomalinoides sp. 1*
	Quinqueloculina cf. Q. laevigata		*Anomalinoide sp. 2*
	Quinqueloculina cf. Q. patagonica		*Cibicidina (?) sp. 1*
	Quinqueloculina cf. Q. neostriatula		*Cibicides cf. C refulegens*
	Quinqueloculina crassicarinata		*Cibicides pseudolobatus*
	Quinqueloculina cuvieriana		*Cibicidiodes mabahethi*
	Quinqueloculina distorqueata		*Cibicidiodes sp. 1*
	Quinqueloculina patagonica		*Conorbella pulvinata*
	Quinqueloculina poeyana		*Cribononion kerguelense*
	Quinqueloculina quinquecarinata		*Cymbaloporetta squammosa*
	Quinqueloculina sp. 1		*Discorbinella chincaensis*
	Quinqueloculina sp. 2		*Dyocibicides sp. 1*
	Quinqueloculina subpolygona		*Dyocibicides sp. 2*
	Spiroloculina communis		*Elphidium aculeatum*
	Spiroloculina corrugata		*Elphidium adventum*
	Spiroloculina parvula		*Elphidium craticulatum*
	Spiroloculina venusta		*Elphidium crispum*
	Triloculina cf. T. quadrata		*Elphidium depressulum*
	Triloculina striatotrigonula		*Elphidium jenseni*
	Triloculina trigonula 4		*Elphidium macellum*
	Triloculina triquetrella		*Elphidium repandus*
	Triloculina cf. T. parisa		*Glabratella patelliformis*
			Glabratella sp. 1
			Heronallenia lingulata
			Lamellodiscorbis dimidiatus
			Neoconorbina terquemi
			Paracibicides edomica
			Pararotalia stellata
			Planoglabratella opercularis
			Planogypsina acervalis
			Planulina sp. 1
			Rosalina sp. 1
			Rotorbinella cf. R. rosea
			Rotorbis mirus
			Rotorboides cf. R. granulosus
			Rugobolivinella pendens
			Siphonina reticulata
			Siphoninoides echinatus
			Siphoninoides laevigatus
			Svratkina sanmiguelensis
			Trichohyalus tropicus

Table 3

Dominant fossil foraminifera of the three Pleistocene formations of the Yalgorup Plain. NB: *** = abundant (>10%), ** = common (>5%), * = uncommon (<5%), - = not recorded. Only species with total sample mean >3 are listed herein; these species are illustrated in Plate 1.

Taxa	Tims Thicket Limestone	Limestone lens (MyalupSand)	Kooallup Limestone
Amphisorus hemiprichii	*	–	*
Marginopora vertebralis	*	–	*
Miliolinella australis	**	*	**
Miliolinella labiosa	*	–	*
Peneroplis planatus	*	–	*
Quinqueloculina baragwanathi	*	–	*
Quinqueloculina poeyana	*	*	*
Quinqueloculina subpolygona	*	*	*
Amphistegina lessoni	**	*	*
Cibicides cf. C. refulgens	***	–	***
Elphidium crispum	**	**	***
Lamellodiscorbis dimidiatus	***	***	***
Pararotalia stellata	*	*	*
Planogypsina acervalis	*	–	**
Rotorbinella cf. R. rosea	**	*	**
Rotorbis mirus	**	*	**
Rotorboides cf. R. granulosus	*	**	*

each sample are presented in Appendix 1. Remanié foraminifera, reworked from older Pleistocene formations, were present in all samples. Remanié foraminifera had a more iron-stained weathered appearance and so were readily distinguishable; hence they were excluded from analyses.

The dominant species recorded from each formation are listed and compared in Table 3 and illustrated in Plate 1. The Tims Thicket Limestone and Kooallup Limestone have hyaline-rich assemblages (65%) with subdominant porcellaneous components. The limestone lens in the Myalup Sand has a hyaline-dominant assemblage (85%) with a minor porcellaneous component. The presence of *A. hemiprichii*, *M. vertebralis*, and *Planogypsina acervalis* in the fossil material confirm that the material is seagrass-derived (Reiss & Hottinger 1984; T A Semeniuk 2000).

The Tims Thicket Limestone and Kooallup Limestone both have very high total foraminiferal densities with greater than 40 000 foraminifera per ml of sediment. The limestone lens in the Myalup Sand has a relatively low foraminiferal density with ca. 250 foraminifera per ml.

Diversity of fossil assemblages

Both Tims Thicket Limestone and Kooallup Limestone assemblages are species diverse, and have even composition. Tims Thicket Limestone and Kooallup Limestone assemblages had at least 90 species present. Fisher indices for the Tims Thicket Limestone and Kooallup Limestone are 22 and 19, respectively. In contrast, the limestone lens in the Myalup Sand had moderate diversity with 35 species recorded for the limited amount of material analyzed. This gives a Fisher index of 11.

Variation in fossil assemblages

Two-way ANOVA on dominant species was used to assess variance in composition between replicate samples of Tims Thicket Limestone and Kooallup Limestones. All species show such lateral variation between replicate

samples that compositional differences between these two Pleistocene limestone formations are not statistically significant. The results of ANOVA are presented in Appendix 2.

Provisional names for fossil assemblages

Each formation has a different assemblage composition, although the two limestone formations have similar dominant species. Definition and nomenclature of foraminiferal assemblages in this study are based primarily on the most abundant species in each formation, but also include species that characterise a particular formation, or species that are volumetrically dominant. For example, the larger foraminifer *M. vertebralis* is volumetrically abundant and conspicuous in the Tims Thicket Limestone and Kooallup Limestone, but is numerically uncommon. Two types of fossil foraminiferal assemblages are documented:

1. a *Marginopora-Amphisorus-Cibicides* assemblage, which characterises the Tims Thicket Limestone and Kooallup Limestone; and

2. a *Lamellodiscorbis-Rotorboides* assemblage, which characterises the limestone lens in the Myalup Sand.

Palaeoecological interpretation

General compositional features of all fossil foraminiferal assemblages are similar to modern assemblages from shallow-water seagrass habitats (T A Semeniuk 2000). They are all hyaline dominant. In fact, the high overlap in species composition between Pleistocene assemblages and live epiphytic assemblages suggests that the major component of the Pleistocene assemblages *was derived from epiphytic foraminiferal species*. The main noteworthy difference between Pleistocene and modern living assemblages is that *Cibicides* cf. *C. refulgens* was not recorded in any of the living assemblages.

In detail, both the Tims Thicket Limestone and Kooallup Limestone have closest similarity to living assemblages at the warmest site of Dongara of T A
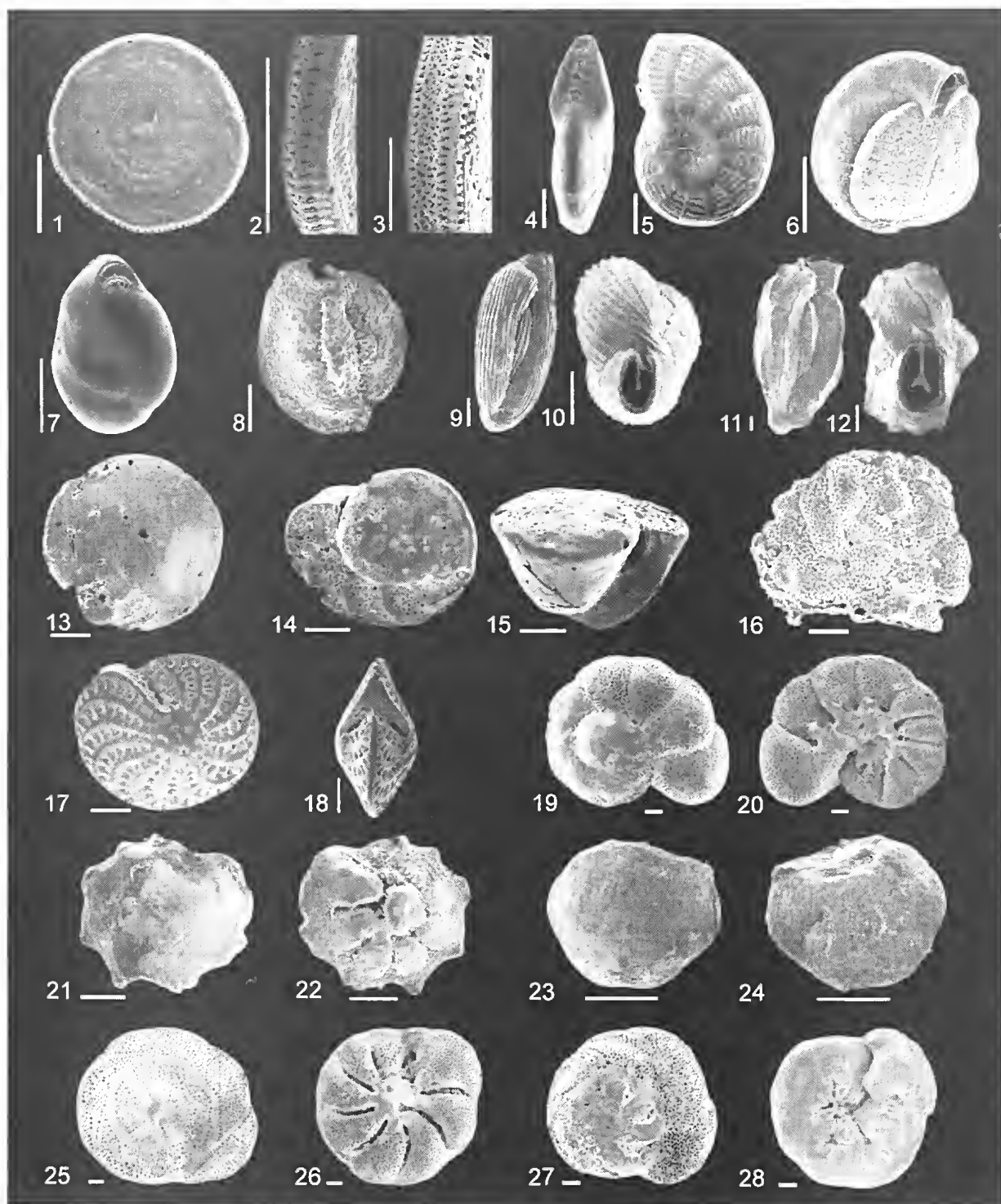
Plate 1. Scanning electron microscope photomicrographs of the foraminifera listed in Table 3. Both Holocene and Pleistocene specimens are used to illustrate the taxonomy. Numbers in brackets indicate the size of the scale bar associated with each foraminifer. 1 *Amphisorus hemiprichii* Ehrenberg, 1839; Dongara, Holocene; Habitus (1.0mm); 2 Aperture (1.0mm); 3 *Marginopora vertebralis* Quoy and Gaimard, 1830; Dongara, Holocene; Aperture (1.0mm); 4 *Peneroplis planatus* (von Fichtel and von Moll, 1798). Dongara, Holocene; Habitus (1.0 mm); 5 Aperture (1.0 mm); 6 *Miliolinella australis* (Parr, 1932); Whitfords, Holocene; Habitus (0. 1 mm); 7 *Miliolinella labiosa* (d'Orbigny, 1839); Albany, Holocene; Habitus (0. 1 mm); 8 *Quinqueloculina baragwanathi* Parr, 1945; Kooallup Limestone, Pleistocene; Habitus (0. 1mm); 9 *Quinqueloculina pocyana* d'Orbigny, 1839; Tims Thicket Limestone, Pleistocene; Habitus (0. 1mm); 10 Aperture (0. 1mm); 11 *Quinqueloculina subpolygona* Parr, 1945; Tims Thicket Limestone, Pleistocene; Habitus (0. 1mm); 12 Aperture (0. 1mm); 13 *Amphistegina lessoni* d'Orbigny, 1826; Tims Thicket Limestone, Pleistocene; Spiral side (0. 1mm); 14 *Cibicides* cf. *C. refulgens* Monfort, 1808; Tims Thicket Limestone, Pleistocene; Spiral side (0. 1mm); 16 *Planogypsina acervalis* (Brady, 1884); Whitfords , Holocene; Spiral side (0. 1 mm); 17 *Elphidium crispum* (Linné, 1785); Tims Thicket Limestone, Pleistocene; Spiral side (0. 1mm); 18 Aperture (0. 1mm); 19 *Lamellodiscorbis dimidiatus* (Jones and Parker, 1862). Albany, Holocene; Spiral side (0. 1 mm) 20 Umbilical side (0. 1 mm); 21 *Pararotalia stellata* (de Férussac, 1827); Kooallup Limestone, Pleistocene; Spiral side (0. 1 mm) 22 Umbilical side (0. 1 mm); 23 *Rotorbinella* cf. *R. rosea* (d'Orbigny, 1826); Myalup Sand, Pleistocene; Spiral side (0. 1 mm) 24 Umbilical side (0. 1 mm); 25 *Rotorbis mirus* (Cushman, 1922); Albany, Holocene; Spiral side (0. 1 mm) 26 Umbilical side (0. 1 mm); 27 *Rotorboides* cf. *R. granulosa* (Heron-Allen and Earland, 1915); Albany, Holocene; Spiral side (0. 1 mm) 28 Umbilical side (0. 1 mm).

Semeniuik (2000, 2001), *i.e.*, 39 and 44 species in common with species at Dongara, respectively. The assemblage from the limestone lens in the Myalup Sand has greatest similarity with living assemblages from an intermediate site of Whitfords of T A Semeniuik (2000, 2001), *i.e.*, 17 species in common.

Tims Thicket Limestone and Kooallup Limestone have at least 7 buliminid taxa and 34 miliolid taxa, compared with 3 buliminid taxa and 10 miliolid taxa recorded for the limestone lens in the Myalup Sand. The number of miliolid taxa recorded in the Tims Thicket Limestone and Kooallup Limestone is similar to the living assemblages at the warmest site at Dongara (around 30 species), whereas the limestone lens in the Myalup Sand is similar to the living assemblages at the coolest site at Albany (both have around 10 taxa). The number of taxa of buliminids in the Pleistocene formations is much reduced; around 3–7 compared with 16–23 recorded in the modern living assemblages, hence, they could not easily be compared.

Larger foraminifera found in the Tims Thicket Limestone and Kooallup Limestone include *A. lessoni, A. hemiprichii, M. vertebralis, P. planatus, Peneroplis pertusus,* and *S. variabilis,* whereas Myalup Sand has only *A. lessoni* present. Again, the Tims Thicket Limestone and Kooallup Limestone had greatest similarity with the living assemblages at the warmest site at Dongara since they all contain the larger benthic species *M. vertebralis, A. hemiprichii, P. planatus* and *S. variabilis.* Additionally, *P. pertusus* and *A. lessoni* were recorded in the fossil assemblages from the Tims Thicket Limestone and Kooallup Limestone. Only one larger foraminifer occurs in the limestone lens in the Myalup Sand.

Compositional comparison of modern assemblages with fossil assemblages using the criteria above suggest that both the Tims Thicket Limestone and Kooallup Limestone were deposited in warm sea water, whereas Myalup Sand accumulated in cooler water.

Discussion and conclusions

The fossil foraminiferal assemblages from the three Pleistocene formations have strong similarity to live epiphytic assemblages from modern seagrass environments and contain the same indicator species for seagrass habitat. This supports the general palaeo-environmental interpretations based on stratigraphic and sedimentary features, and molluscan fauna (Semeniuk 1996), that the shallow-marine units of Tims Thicket Limestone and Kooallup Limestone are seagrass-bank deposits. Palaeoecological reconstructions based on modern foraminiferal assemblages indicate that there are significant sea-temperature differences in the depositional settings of the three Pleistocene formations. Criteria useful for interpreting the sea-temperature setting of the seagrass material include the miliolid fraction, the number of species of larger benthic foraminifera, and the presence or abundance of specific indicator species such as *S. variables;* which all show an increase in abundance with more tropical conditions (T A Semeniuk 2001). The significant reduction in buliminid content of fossil assemblages and common occurrence of broken tests in fossil material suggest that post-mortem processes have affected the preservation of these more fragile taxa and that this criterion is not useful for reconstructing palaeoclimate settings.

Sea-temperature estimates

A number of studies previously have used modern larger benthic foraminiferal assemblages to infer climate setting in Holocene to Tertiary successions (*e.g.,* Reiss & Hottinger 1984; Murray 1987, 1991; Adams *et al.* 1990). Tropical climates are inferred using both specific shallow-water benthic tropical species or symbiont-bearing larger foraminifera (Reiss & Hottinger 1984; Adams *et al.* 1990). Symbiont-bearing larger foraminifera are an informal group of unrelated taxa. Adams *et al.* (1990) include the genera *Amphistegina, Amphisorus, Marginopora, Peneroplis* and *Sorites* as part of this group, and these species also are considered in this study. The modern distributions of these taxa are confined to an equator-centered area bounded to the south and north by the 18–20°C isotherm for the warmest month of the year, restricting these taxa to sub-tropical and tropical regions (except where warm currents influence their distributions).

The number of species of larger foraminifera decreases away from equatorial regions, forming a gradational distribution pattern about the equator, symmetrical in both northern and southern hemispheres (Adams *et al.* 1990). The number of species of larger foraminifera can be used as an index of tropical conditions, and specific taxa can be used to infer minimum winter temperatures. For example, *A. hemiprichii* has a present-day biogeographic limit corresponding to a minimum winter isotherm of 17°C (Reiss & Hottinger 1984) and *A. lessoni* has a biogeographic limit corresponding to a minimum winter isotherm of 14°C (Larsen 1976). It is pertinent to compare these findings with those of the present study. Using the presence/absence of *A. hemiprichii* as an index of tropical conditions, the results of this study suggest that the Tims Thicket Limestone and Kooallup Limestone were deposited in seas with temperatures greater than 17°C, whereas the Myalup Sand accumulated in seas with temperatures lower than 17°C, but greater than 14°C.

Sea temperatures and carbonate productivity

In the palaeogeographic reconstruction of Pleistocene conditions on the Yalgorup Plain by Semeniuk (1996), changes in sedimentation style from carbonate-rich prograded beach-ridge plains to quartz-rich barrier dune systems were attributed to changes in carbonate productivity linked to sea-temperature changes, or to the variable influx of quartz sand, which diluted *in situ* carbonate production. Foraminiferal diversity indices and other compositional assemblage criteria that are sensitive to climate setting have corroborated that these differences are at least in part due to sea-temperature changes. Specifically, the diversity of fossil assemblages correlates well with carbonate abundance in these Pleistocene limestone formations. There were high species counts (high diversity) in limestones with high abundance of carbonate grains, representing periods of high carbonate production, whereas there are low species counts (moderate diversity) for the localised carbonate

layers in quartz sand-rich formations, representing times of minimal carbonate production. Although carbonate content alone could be a reflection of palaeogeographic setting, the high diversity of selected foraminifera taxa is correlated with warm sea-temperatures.

Pleistocene sea-temperature record

The differences in fossil foraminiferal assemblages from the Pleistocene formations appear to record changes in palaeo sea-temperature differences through time. In particular, the succession of limestones and quartz-rich sands under the Yalgorup Plain records a warm-cool-warm cycle of carbonate deposition during the late Pleistocene. Cycles of warm-water and cool-water sedimentation also were proposed by Kendrick et al. (1991) in order to explain the general alternation of quartz-rich and carbonate-rich sedimentation in the Pliocene to Pleistocene along the Western Australian coast, and by Semeniuk (1996) to explain the changes in sedimentation style in the development of the Yalgorup Plain.

In theory, three mechanisms could have triggered warmer and cooler sea-temperature phases along the Western Australian coast during Pleistocene interglacials. Firstly, climate change related to Milankovich cycles may have generated more southern tropical zones along the coast. Secondly, changing strength of a palaeo-Leeuwin Current (as proposed by Cann & Clarke 1993; Wells & Wells 1994) may have elevated winter water temperatures in a narrow zone close to the coast (the Leeuwin Current in the modern setting is a warm low salinity oceanic current, dominant during autumn and winter, that flows southwards along the inner shelf from the warm water tropical regions of Western Australia to the cooler water temperate regions; Cresswell 1991). Lastly, changes in sea level may have generated a Rottnest-type setting (in which warmer-water isotherms linked to the Leeuwin Current were intersected at greater distance from the coast). There is no supporting palaeogeographic or foraminiferal facies evidence for this last hypothesis. The evidence for different mechanisms to sea-temperature change along the Western Australian coast, acting independently and in combination, is discussed below.

Milankovich cycles can occur within less than 100,000 yrs (Berger 1988; 1992). Hence, it is possible that the changing climate conditions documented for the Pleistocene formations from the Yalgorup Plain represent such cyclicity. This hypothesis cannot be evaluated until the Pleistocene formations from the region are accurately dated to determine whether this cyclicity is correlated with known astronomical forcing intervals. In addition, there is strong palaeoclimate evidence from South Australia and off-shore drill core material from Northern Western Australia that the strength of the Leeuwin Current changes with climate (McGowran et al. 1997; Okada & Wells 1997), and hence their mutual effect on foraminiferal distributions cannot be completely decoupled.

A change in strength of the Leeuwin Current could be triggered by sea-level change associated with tectonic activity or by climate change. If the Leeuwin Current had a greater nearshore influence during interglacial times this would account for a warmer sea-temperature fauna at more southern latitudes than at present, since elevated winter temperatures would allow tropical species to move further south. The interpretation and reconstruction of the palaeo sea temperature from shallow water deposits, based on the fossil foraminifera in this case, may not point to marked regional climate change, but rather to the changing influence of the Leeuwin Current. In order to establish the cause for such a change in current strength, the palaeohistory of the Leeuwin Current would need to be corroborated with other evidence for sea-level and climate change.

The Pleistocene history of the Leeuwin Current has been investigated by a number of authors. Cann & Clarke (1993) attributed the abundance of *M. vertebralis* (which normally has tropical affinity) in last interglacial sediments from Spencer Gulf Region, South Australia, to the presence of a palaeo Leeuwin Current. They postulated that this Current had greater ecological influence across the continental coast in South Australia at times of global warming and at higher sealevels. Other neritic benthos, nektonic nautiloids, and planktonic foraminifera within the Gulf show exhibit similar changes in their biogeographic ranges, consistent with transport of warmer waters by the Leeuwin Current in the last interglacial (McGowran et al. 1997). Faunal successions in planktonic foraminifera suggest the current intensifies during interglacials and weakens or ceases during glacial periods on time scales of ca 10^5 yr. This idea is supported by the work of Wells & Wells (1994) on planktonic foraminifera in deep-sea cores from offshore Western Australia. They determined sea-surface temperatures and gradients during the last 130 ka, concluding that during the last interglacial maximum, sea-surface temperatures were similar to those of today in summer and up to 3° C warmer in winter. Wells & Wells (1994) postulated that the Leeuwin Current flowed as an intensified current in a narrow zone close to the coast during the last interglacial maximum. Nanofossil records from these deep-sea cores suggest a weakening or cessation of the Leeuwin Current for glacial periods (Okada & Wells 1997).

Studies in both these regions suggest that the Leeuwin Current was more intense during the last interglacial and that the intensity of the current reflects climate. Thus, it is most likely that interplay of these mechanisms occurred to generate the Pleistocene warm-cool-warm cycle of carbonate deposition in shallow water settings in southwestern Australia, *i.e.*, increased activity of a palaeo-Leeuwin Current accompanied changes in sea-level and climate.

This study compared foraminiferal assemblages from local Pleistocene seagrass-bank deposits of southwestern Australia to Holocene equivalents. It utilised the variation in composition of modern living foraminiferal assemblages with respect to climate setting to interpret the fossil assemblages. There are many Quaternary coastal marine sequences documented around the globe that show similarity of sedimentary style, facies, and climate setting between local Holocene and Pleistocene deposits that would be suitable for palaeoecological reconstruction using the approach outlined in this study. In order to apply this approach globally, it is first necessary to document compositional changes in modern foraminiferal assemblages for a single habitat in

relationship to a regional or sub-regional climate gradient. The work reported in this paper suggests that there is scope to refine the palaeoecological reconstructions of Pleistocene sequences to a greater level than has hitherto been recorded in the literature.

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Appendix 1

Results of species counts from Pleistocene samples.

Order	Taxa	Sampling sites (see key below)						
		TT1	TT2	TT3	MS1	KL1	KL2	KL3
Textularia								
	Gaudryina sp. 1	0	0	1	0	1	0	0
	Textularia pseudogramen	1	0	0	0	0	0	0
	Textularia cf. T. sagittula	1	0	0	0	0	0	0
	Textularia sp 1	1	0	0	0	0	0	0
Miliolina								
	Amphisorus hemiprichii	12	1	3	0	12	4	0
	Biloculinella sp. 1	3	3	1	0	1	1	1
	Cornuspira involvens	0	0	0	0	1	0	1
	Cornuspira sp. 1	0	3	0	0	0	0	2
	Cornuspira acicularis	0	0	0	0	3	3	2
	Marginopora vertebralis	11	0	6	0	8	8	0
	Miliolinella australis	4	29	16	10	16	16	15
	Miliolinella labiosa	2	12	4	0	0	0	6
	Miliolinella sp. 1	0	3	6	0	3	0	3
	Nubecularia luciuga	0	0	0	0	0	1	1
	Parrina bradyi	0	0	0	0	1	0	2
	Peneroplis pertusus	2	0	0	0	1	0	0
	Peneroplis planatus	10	6	7	0	6	0	0
	Pseudomassilina australis	1	0	0	0	0	0	0
	Pseudotriloculina subgranulata	0	0	1	2	2	0	0
	Pyrgo sarsi	0	0	4	0	0	1	0
	Quinqueloculina baragwanathi	1	6	5	0	0	0	18
	Quinqueloculina carinata	0	2	0	0	0	0	2
	Quinqueloculina cf. Q. bicarinata	1	1	0	0	0	0	0
	Quinqueloculina sulcata	0	1	1	0	0	0	0
	Quinqueloculina cf. Q. incisa	3	3	8	0	2	2	2
	Quinqueloculina cf. Q. laevigata	1	3	3	0	6	1	4
	Quinqueloculina cf. Q. patagonica	1	1	0	0	0	0	0
	Quinqueloculina cf. Q. neostriatula	5	3	3	0	1	1	0
	Quinqueloculina crassicarinata	0	0	0	0	1	3	1
	Quinqueloculina cuvieriana	0	0	0	4	1	0	0
	Quinqueloculina distorqueata	0	0	1	0	1	1	1
	Quinqueloculina patagonica	0	0	0	0	1	0	3
	Quinqueloculina poeyana	6	0	8	1	2	5	2
	Quinqueloculina quinquecarinata	7	3	0	1	0	0	4
	Quinqueloculina sp. 1	3	3	1	1	2	0	0
	Quinqueloculina sp. 2	0	1	2	1	2	0	2
	Quinqueloculina subpolygona	7	4	10	1	3	1	4
	Spiroloculina communis	1	0	0	0	0	0	0
	Spiroloculina corrugata	2	2	1	0	1	0	4
	Spiroloculina parvula	0	1	0	0	0	0	0
	Spiroloculina venusta	0	0	0	0	0	0	3
	Triloculina striatotrigonula	4	2	5	1	2	3	0
	Triloculina trigonula	4	0	2	4	1	8	0
	Triloculina triquetrella	5	3	2	0	1	0	0
	Triloculinella cf. T. parisa	1	8	1	0	1	1	0
Rotaliina (spirillinids)	*Patellina corrugata*	0	1	4	0	0	0	2
	Planispirillina spinigera	1	2	0	0	1	0	2
	Spirillina limbata	0	3	0	0	0	0	0
	Spirillina sp. 1	0	0	0	0	0	0	1
(lagenids)	*Fissurina bradyformata*	0	1	0	0	0	0	0
	Sigmoidella elegantissma	1	0	0	0	0	0	0
(buliminids)	*Bolivina sp. 1*	0	0	0	0	0	0	2
	Bolivina sp. 2	0	0	0	0	1	0	2
	Bolivina quadrilatera	0	0	0	0	0	0	1
	Buliminoides williamsonianus	0	0	0	0	0	0	1
	Elongobula andromache	0	0	0	0	1	0	0
	Fijiella simplex	0	0	1	1	0	0	2
	Loxostoma cf. L. digitale	0	4	0	1	3	0	0
	Loxostomina costulatum	1	0	5	0	0	1	0
	Loxostomina limbata	0	1	2	0	0	1	1
	Pavonina flabelliformis	0	0	0	0	1	0	0

Order	Taxa	Sampling sites (see key below)						
		TT1	TT2	TT3	MS1	KL1	KL2	KL3
	Reussella armata	0	1	2	1	2	1	0
	Reussella simplex	0	1	0	0	0	2	0
	Saidovina sp. 1	0	0	1	0	0	0	0
	Sigmavirgulina tortuosa	0	0	0	0	0	0	2
	Trifarina sp. 1	0	0	0	0	1	0	0
(rotallids)	*Acervulina mahabeti*	1	0	2	0	0	0	0
	Amphistegina lessoni	16	10	11	1	30	9	3
	Angulodiscorbis quadrangularis	1	2	0	0	0	0	2
	Annulopatelinella annularis	0	0	0	0	0	0	2
	Anomalinoides globosus	10	2	0	3	3	11	1
	Anomalinoides sp. 1	1	0	1	0	0	0	0
	Anomalinoide sp. 2	0	0	0	0	0	0	1
	Cibicidina (?) sp. 1	0	0	0	0	1	0	0
	Cibicides cf. C refulegens	37	43	60	0	41	81	24
	Cibicides pseudolobatus	0	1	2	8	1	0	1
	Cibicidiodes mabahethi	0	0	0	0	1	3	2
	Cibicidiodes sp. 1	0	0	0	15	0	0	0
	Conorbella pulvinata	0	1	1	2	0	0	2
	Cribononion kerguelense	1	0	0	0	0	0	0
	Cymbaloporetta squammosa	0	0	1	0	0	0	0
	Discorbinella chincaensis	0	0	0	0	0	0	1
	Dyocibicides sp. 1	0	1	6	0	2	0	3
	Dyocibicides sp. 2	8	1	1	3	0	0	0
	Elphidium aculeatum	0	0	1	1	1	0	0
	Elphidium adventum	1	0	1	1	3	2	1
	Elphidium craticulatum	2	0	0	9	2	4	0
	Elphidium crispum	30	16	29	19	30	53	15
	Elphidium depressulum	0	1	2	0	0	0	0
	Elphidium jenseni	3	4	3	5	1	2	1
	Elphidium macellum	3	2	5	0	2	0	3
	Elphidium repandus	0	0	2	0	0	0	1
	Glabratella patelliformis	0	2	4	0	3	4	4
	Glabratella sp. 1	0	1	0	1	0	0	0
	Heronallenia lingulata	0	0	0	0	0	0	2
	Lamellodiscorbis dimidiatus	51	17	34	67	41	55	24
	Neoconorbina terquemi	0	1	0	0	1	2	2
	Paracibicides edomica	0	0	0	15	0	0	0
	Pararotalia stellata	1	1	0	1	6	11	3
	Planoglabratella opercularis	0	1	1	0	0	0	0
	Planogypsina acervalis	1	4	0	0	13	0	49
	Planulina sp. 1	0	2	2	1	4	5	1
	Rosalina sp. 1	0	0	0	2	0	0	0
	Rotorbinella cf. R. rosea	4	21	10	4	6	4	17
	Rotorbis mirus	14	7	8	1	2	12	9
	Rotorboides cf. R. granulosus	5	3	4	27	8	2	1
	Rugobolivinella pendens	0	1	0	0	0	0	0
	Siphonina reticulata	1	0	0	0	0	0	1
	Siphoninoides echinatus	0	0	0	0	1	0	1
	Siphoninoides laevigatus	0	0	1	0	0	1	0
	Svratkina sanmiguelensis	1	0	0	0	1	0	0
	Trichohyalus tropicus	0	0	0	0	0	0	1

TT1 = Site 1 (Tims Thicket Limestone) replicate sample 1
TT2 = Site 1 (Tims Thicket Limestone) replicate sample 2
TT3 = Site 1 (Tims Thicket Limestone) replicate sample 3
MS1 = Site 2 Myalup Sand sample
KL1 = Site 3 (Kooallup Limestone) replicate sample 1
KL2 = Site 3 (Kooallup Limestone) replicate sample 2
KL3 = Site 3 (Kooallup Limestone) replicate sample 3

Appendix 2

Two-way ANOVA results for lateral variation in species from the Tims Thicket Limestone and the Kooallup Limestone for species with sample mean > 3.

Taxa	F value	P value	F-critical
Amphisorus hemiprichii	0	1	7.7086
Marginopora vertebralis	0.0064	0.9398	7.7086
Miliolinella australis	0.0085	0.9309	7.7086
Miliolinella labiosa	1.2	0.3348	7.7086
Peneroplis planatus	4.05	0. 1145	7.7086
Quinqueloculina baragwanathi	0. 1043	0.7628	7.7086
Quinqueloculina poeyana	0.4098	0.5569	7.7086
Quinqueloculina subpolygona	4.9706	0.0897	7.7086
Amphistegina lessoni	0.0394	0.8522	7.7086
Cibicides cf. C. refulgens	0.0120	0.9180	7.7086
Elphidium crispum	0.4126	0.5556	7.7086
Lamellodiscorbis dimidiatus	0.2038	0.6751	7.7086
Pararotalia stellata	6.48	0.0636	7.7086
Planogypsina acervalis	1.6695	0.2659	7.7086
Rotorbinella cf. R. rosea	0. 1730	0.6988	7.7086
Rotorbis mirus	0.2951	0.6158	7.7086
Rotorboides cf. R. granulosus	0.2174	0.8899	7.7086

* indicates F value is greater than F-critical

Endozoochory and the Australian bluebell: consumption of *Billardiera fusiformis* (Labill.) Payer (Pittosporaceae) seeds by three mammal species at Two Peoples Bay Nature Reserve, Western Australia.

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Abstract

Animals that feed on fruits have the potential to play a key role in vegetation dynamics, assisting in plant succession and maintenance of floral diversity. Seeds may be ingested, passed through the gut and voided to the soil. Through this action seeds are dispersed to new sites (endozoochory). Removal of pulp from fleshy fruits during transport through the gut may also assist in the stimulation of germination. This study compared the germination response of seeds of the Australian bluebell, *Billardiera fusiformis*, retrieved from faecal pellets of three native mammals (quokka *Setonix brachyurus*, Gilbert's potoroo *Potorous gilbertii* and bush rat *Rattus fuscipes*) with that of freshly collected and aged, but non-ingested seeds, from Two Peoples Bay Nature Reserve, Western Australia. Ingestion of seeds of *B. fusiformis* by quokkas, Gilbert's potoroos and bush rats increased germination by 58%, 31% and 2% respectively over a control (seeds physically removed from freshly collected fleshy fruit). When placed in dry storage for over a year, however, both ingested and non-ingested seeds displayed significant increases in percent germination.

Keywords: endozoochory, fleshy fruit, seed dispersal, gut passage, animal faeces

Introduction

Seed dispersal is important for reproductive success and is the critical mobile stage of a plant's life history. Dispersal may be accomplished through a variety of mechanisms and agents including wind, water, ballistics and animals. The main animal vectors of seed dispersal are vertebrates (especially mammals and birds) and ants. Animals have the ability to move seeds to new sites passively either on body surfaces (epizoochory) or actively by consuming fruits (endozoochory) or caching seeds. They may also play an active role in seed dispersal through digging and burrowing activities (Chambers & McMahon 1994). Diggings can trap plant litter, forming nutrient-rich microsites for the germination of seeds (Martin 2003). This soil disturbance is important in nutrient cycling and contributes to soil health (Martin 2003, Garkaklis *et al.* 2004). In Western Australia many small mammals create soil disturbance through their foraging for seeds, fungi, roots and invertebrates, or through burrowing activity. Seeds and spore-filled fruiting bodies of hypogeal fungi, such as those consumed by Gilbert's potoroos, are ingested, passed through the gut and voided to the soil (Nguyen *et al.* 2004).

Frugivores have an effect on the germination of seeds (rate and percent) in about 50% of plants they consume (Traveset 1998). In many cases only a proportion of ingested seeds survive passage through the gut, with larger seeds suffering damage. Ingestion of seeds may increase their germinability by removal of dormancy. The removal of fleshy pulp prior to laboratory incubation of seeds has increased germination in a number of species (e.g., *Persoonia* spp, *Leucopogon verticillatus*), suggesting that germination inhibitors may be present in the flesh (Baskin & Baskin 2001). The removal of fleshy fruit material from around seeds may also act to prevent seeds from being destroyed by bacteria before germination occurs (Witmer 1991). Passage through the gut may alter the seed coat or endocarp, aiding water permeability and thereby affecting germination through the action of chemicals or mechanical action (Baskin & Baskin 2001). Survival in the gut may also be dependent on seed size (Moussie *et al.* 2005).

The movement of seeds away from parent plants through zoochory can also have beneficial effects – colonisation of new areas, escape from seedling mortality near parent plant due to competition between parent and seedlings, and the creation of wider population genetic structure (Samuels & Levey 2005). Dispersal distance will be dependent on the foraging range of the animal disperser and, in the case of endozoochory, its gut retention time. The sum of these effects may play a key role in vegetation dynamics, and may be a significant force in plant succession and maintenance of floral diversity.

Amongst the multitude of studies on endozoochory and seed germination (e.g., Milton & Dean 2001; Traveset *et al.* 2001; Paulsen & Hogstedt 2002; Stanley &

Lill 2002; Cosyns et al. 2005a,b; Couvreur et al. 2005; Mouissie et al. 2005) the majority have investigated the effects of ingestion of seeds in birds, rabbits or ungulates such as deer, donkeys and sheep, and few have been conducted in Australia. Traveset et al. (2001) and Barnea et al. (1991) reported differences in germination after passage through bird guts, dependent on species and gut retention time. Paulsen & Hogstedt (2002) reported increased seedling emergence after passage of seeds through birds; Stanley & Lill (2002) reported high viability after passage of native Rhagodia seeds through the gut of silvereyes (Zosterops lateralis). Williams et al. (2000) investigated the effect of ingestion of weed seeds by introduced rodents and possums on survival and subsequent germination of those seeds and considered that there was a major potential for ship rats (Rattus rattus) and brushtail possums (Trichosurus vulpecula) to disperse weed seeds in New Zealand. Native foxes (Pseudalopex culpaeus) have also been implicated in the spread of weed species in Chile through consumption of alien fruits and their defaecation (Silva et al. 2005).

Jordano (1992) reported that between 82% and 88% of woody plants in Australian tropical and subtropical regions have fruits or seeds that are dispersed by vertebrates. The majority of these fruits are fleshy and are probably bird or bat dispersed, with few plant species having seeds adapted for dispersal by ground-foraging mammals or birds such as the cassowary (Casuarius casuarius) (Willson et al. 1989).

A number of Australian studies have investigated the relationship between endozoochory, seed germination and non-flying mammals. These include McGrath & Bass (1999) and Noble (1975) who investigated the ingestion and dispersal of seeds by the emu (Dromaius novaehollandiae) in New South Wales. Webber & Woodrow (2004) studied the effect of cassowary frugivory on seed germination of a rare rainforest tree in Queensland. There has been some investigation of caching of seeds by woylies (Bettongia penicillata) in Western Australia and their effect on seedling establishment (Murphy et al. 2005), and Parsons (1997) reported that Carpobrotus seeds from rabbit (Oryctolagus cuniculus) and eastern grey kangaroo (Macropus giganteus) faeces germinated readily in comparison to fresh seeds. In general though, the importance of non-flying mammals as agents of seed dispersal in Australia has been neglected. Fleshy fruits and endozoochory may be common in tropical and subtropical rainforests in Australia, but in most Australian sclerophyll woodlands and heaths less than 30% of plant species have fleshy fruits (Willson et al. 1989). In south western Australian plant communities seed dispersal by vertebrates is considered uncommon due to the low incidence of seeds enclosed by fleshy fruits (Bell 1994).

The objective of this study was to investigate and quantify plant-animal interactions associated with seed consumption. This paper reports the relationship between small native ground-dwelling mammals (quokka Setonix brachyurus, Gilbert's potoroo Potorous gilbertii and bush rat Rattus fuscipes) and seeds of the Australian bluebell, Billardiera fusiformis, (formerly Sollya heterophylla) in a Western Australian south coast nature reserve.

Methods

Study site

The study site is the Mount Gardner promontory within Two Peoples Bay Nature Reserve, situated 30 km east of Albany on the southern coastline of Western Australia. The site consists of granite headlands, small indented bays and hills covered in low heath vegetation. The area is an important refuge for threatened fauna, including the only known habitat of the critically endangered Gilbert's potoroo. Other native ground-dwelling mammals resident in the area include the quokka, bush rat, and quenda (Isoodon obesulus). The vegetation is comparable to other coastal sites and has been long impacted by the introduction of the plant pathogen, Phytophthora cinnamomi (Orr et al. 1995). Flora species abundant in the area include Agonis flexuosa, Eucalyptus marginata, E. calophylla, Allocasuarina fraseriana, Melaleuca striata, Adenanthos barbigeros, Hakea ferruginea, Jacksonia spinosa and Leucopogon species, with numerous sedges (e.g., Anarthria scabra) that provide important understorey cover for small mammals.

Faecal samples

A total of 275 scats from quokkas, Gilbert's potoroos, bush rats and quendas were assessed from the study site between September 2003 and February 2004. Samples comprising one or more fresh scats were taken from cage traps during trapping sessions to monitor the Gilbert's potoroo population, and opportunistically collected (in the case of quokka faeces) in the general vicinity of the trap lines. Scats were air dried as soon as possible after collection, weighed and seeds manually extracted from faeces. Seed type and load per scat were recorded and the mean number of seeds per scat and per gram of scat calculated for each mammal species.

Seed germination

Seeds retrieved from scats were identified by comparison with seeds found on plants in the study area. Seeds of Billardiera fusiformis were germinated as they were the only seeds found in the scats of more than one mammal species. Seeds were incubated without treatment on filter paper over moistened sponge (5 ml deionised water) in 90 mm Petri dishes in an incubator at 15°C with a 12 hour photoperiod. The experiment consisted of three replicates of 20 (quokka, bush rat and control), and 15 (Gilbert's potoroo) seeds from freshly retrieved seeds. In addition to germinating seeds from freshly collected faecal matter, seeds recovered from faeces were germinated after more than one year of storage (approx. 15 months in dry storage at 21°C). Where enough seeds were available a smoke treatment was applied to aged seeds (bush rat and Gilbert's potoroo only). This treatment consisted of soaking seeds for 24 hours in a 10% solution of Smokemaster® and rinsing seeds in deionised water prior to incubation as above. Each treatment contained four replicates of 25 seeds. Germination trials were concluded after 124 days.

In order to compare germinability of ingested seeds with that of non-ingested seeds, we incubated freshly collected and aged seeds of Billardiera fusiformis under the same conditions. Prior to incubation fleshy material

was removed from seeds by rubbing flesh away from seeds under water. Flesh was also removed from seeds before storing dry in paper bags for over 15 months at room temperature (approx 21°C and 50% relative humidity). Seeds were incubated without treatment (control) and under five different treatments (Table 4). Germination trials were concluded after 127 days.

Data Analyses

Percent germination data were arcsine square root transformed prior to Analysis of Variance (ANOVA) using StatView®. Mean time to germination (MTG) was calculated for the treatments that gave maximum germination for each species, using the equation:

$$MTG = \Sigma \, (nd) \, / \, N$$

where: n = number of seeds germinated between scoring intervals; d = the incubation period in days at that time point and N = total number of seeds germinated.

Results

Faecal analysis

Seed material was found in less than one third of the faecal samples from quokkas, Gilbert's potoroos and bush rats. Scats ranged in weight and number of seeds retrieved (Table 1). There was no visible evidence of damage to seeds and the only type of seeds common to all three mammals was the Australian bluebell, *Billardiera fusiformis* (Labill.) Payer (Pittosporaceae). *Billardiera fusiformis* is an evergreen climber with blue bell-shaped flowers and cylindrical fleshy drupe containing 30–50 seeds embedded in the mucilaginous pulp. This species is endemic to Australia and is commonly found in temperate regions of WA, SA, NSW and Tasmania. Scats of bush rats contained greater numbers of *B. fusiformis* seed per gram than those of either quokkas or Gilbert's potoroos, with more than 30

seeds retrieved per gram (Table 1). Only potoroo samples contained seeds of other plant species (*Marianthus* sp., *Astroloma* sp. and *Leucopogon* sp.) No seeds were recovered from the 57 quenda scats examined.

Seed germination

Ingested seed

Percentage germination of freshly retrieved seeds of *Billardiera fusiformis* was highest in seeds retrieved from quokka scats (58%) and lowest in seeds retrieved from bush rat scats (2%), with 31% germination of seeds retrieved from faecal pellets of Gilbert's potoroo (Table 2).

First germination occurred after 21 days for seeds recovered from both quokka and Gilbert's potoroo faeces. Ageing increased percentage germination of seeds ingested by Gilbert's potoroos and bush rats, but not quokkas. Treating aged ingested seeds with smoke compound further increased germination (Table 2). An estimation of the numbers of germinable seeds per gram of faecal matter was made for both fresh and aged seeds retrieved from faecal material. Germinable seeds per gram dry weight of faecal matter increased from 1.95 (fresh) to 1.66 (aged) in quokka and 0.14 (fresh) to 0.22 (aged) in Gilbert's potoroo. After ageing, there was a five-fold increase in germination of *B. fusiformis* seeds ingested by bush rats (from 0.75 to 4.80 germinable seeds per gram dry weight of faecal matter).

Non-ingested seed

Fresh non-ingested seeds of *B. fusiformis* were dormant on collection. Laboratory treatment of seeds increased germination, as did ageing (Table 3). Application of smoke stimulated some germination (12%) as did the combined effects of heat shock and smoke (28%). Heat shock alone did not provide a cue for germination, and limited germination occurred after the application of potassium nitrate.

Table 1

Occurrence of *Billardiera fusiformis* seeds in scats of four ground-dwelling mammals at Two Peoples Bay Nature Reserve, Western Australia.

Species	Total no. scats	Mean scat weight (g) n=10	Total scat dry weight (g)	Total no. *B. fusiformis* seeds retrieved	Mean no. seeds per scat (range)	No. seeds of *B. fusiformis* per g of scat
Quokka	16	1.076	19.48	66	4.13 (0-29)	3.4
Gilbert's potoroo	141	0.361	41.01	18	0.13 (0-4)	0.4
Bush rat	61	0.038	2.61	79	1.29 (0-20)	30.3
Quenda	57	0.210	19.10	0	0	0

Table 2

Percentage germination of *Billardiera fusiformis* seeds retrieved from faecal samples (fresh and aged) collected between September 2003 and February 2004 compared to seeds collected from plants (control).

	Gilbert's potoroo	Quokka	Bush rat	Control
Fresh (no treatment)	31 ± 9.2	58 ± 1.4	2 ± 11.3	0
Fresh (+ smoke)	n/a	n/a	n/a	12 ± 1.6
Aged 15+mths (no treatment)	50 ± 12.8	49 ± 7.7	32 ± 4.2	16 ± 5.3
Aged 15+mths (+ smoke)	62 ± 5.0	n/a	64 ± 4.4	91 ± 3.4

Table 3

Treatment conditions and results of laboratory germination of fresh and aged seeds of *Billardiera fusiformis*.

Treatment Type	Condition	Percent Germination Fresh seeds	Stored seeds 15 mths
Control	No treatment	0	16
Heat shock	68 hours at 80°C	0	53
Smoke	2 ml Smokemaster ® on filter paper	12	91
Gibberellic acid	2 ml Gibberellic acid as GA_3 on filter paper	0	8
Heat shock + Smoke	68 hrs 80°C + 2 ml Smokemaster ® on filter paper	28	93
Potassium nitrate	2 ml KNO_3 at 100 mg/L^{-1} on filter paper	2	47

Table 4

Results of two way ANOVA comparing the effects of ageing and smoke treatment and the interaction of these variables on percent germination in *Billardiera fusiformis*.

Source of variation	df	Mean square	F	Significance
Ageing	1	1.701	24.778	<.0001
Treatment	1	0.286	4.165	0.0477
Ageing x treatment	1	0.689	10.030	0.0029

When smoke was applied to aged non-ingested seeds germination reached 91%. Germination was also high (93%) when heat shock and smoke were applied sequentially, although heat shock alone produced only 53% germination in aged non-ingested seeds. The application of potassium nitrate (KNO_3) to non-ingested seeds increased germination to 47%. Ageing of both ingested and non-ingested seeds had a highly significant effect on percent germination (Table 4). There was also a significant interaction between ageing and smoke treatment on percent germination of both freshly collected and ingested seeds of *B. fusiformis*.

Time to first germination for non-ingested aged seeds was 23 days, and similar to first germination for ingested aged seeds (25 days). Mean time to germination was greater than 30 days for all but non-ingested aged and smoke-treated seeds (Table 5).

Discussion

This investigation has demonstrated that a functional relationship exists between mammals at Two Peoples Bay and the Australian bluebell, *Billardiera fusiformis*. It has highlighted the presence of inter-specific differences

Table 5

Mean time to germination (days) for fresh and aged ingested and non-ingested seeds of *Billardiera fusiformis*.

	Ingested			Non-Ingested
	Gilbert's potoroo	Quokka	Bush rat	
Fresh	31.1	37.4	42.0	-
Fresh + smoke	-	-	-	60.0
Aged	39.0	30.5	43.1	33.6
Aged + smoke	41.6	-	44.9	25.3

between dispersers with respect to their effects on seed germination. The significant differences seen in germination response of seeds from faeces of the three mammal species reflect differences in digestive tract morphology and gut retention time. Like other species of *Rattus*, bush rats have a relatively simple digestive system and short gut passage time. Both potoroos and quokkas exhibit foregut fermentation, but in potoroos the peptic hindgut is more important in digestion and digesta do not remain as long in the forestomach as in macropodids including the quokka (Hume & Carlisle 1985). Gut passage time is greater in the quokka at 38 hours (Calaby 1958) than the 24–30 hours observed in other potoroids, the long-nosed potoroo *Potorous tridactylus*, rufous bettong *Aepyprymnus rufescens* and woylie (Wallis 1994).

Frugivores may provide an essential service by freeing seeds from fruit pulp in addition to their role as seed dispersers. Release from germination inhibitors and high osmotic pressures by removal of flesh are mechanisms that can alter germination rate or percent (Samuel & Levey 2005). The removal of pulp from *B. fusiformis* seeds occurred much more rapidly through gut passage compared to natural fruit pulp decomposition that may take several months (pers. obs. A Cochrane). Little of the fleshy fruit was removed during passage of seeds through the gut of bush rats, perhaps contributing to reduced germination amongst seeds that they have eaten. The type of food ingested with the fruits may also affect germination by chemical and mechanical abrasion of the seed coat (Traveset 1998). The different speeds of germination promoted by different rates of gut passage may increase the probability that seeds will recruit successfully at a given time and in a given place (Traveset *et al.* 2001). Early seedling emergence in unpredictable environments may assist in maximising seedling survival.

For the most part, endozoochory provides an advantage for germination of *B. fusiformis* through partial release of dormancy in "fresh" seeds. Chemical and mechanical abrasion and de-pulping of seeds have apparently combined with the moist environment of the faeces to partially overcome dormancy. Germination was greater and more rapid in seeds retrieved from scats than in freshly collected seeds. Germination was also greater in seeds collected from plants and aged, indicating an after ripening requirement that implies the presence of primary dormancy (Mandujano *et al.* 1997). *B. fusiformis* has a rudimentary embryo within a white granular endosperm, often referred to as underdeveloped (Baskin

& Baskin 2001). The embryo is small and consequently has to grow before the seeds can germinate. Growth of the embryo takes places after the fruits have fallen. Dormancy delays germination until favourable conditions are met for seedling establishment and growth. For *B. fusiformis* smoke and seed ageing were partner cues for germination in the absence of ingestion to break dormancy. Smoke has been reported to cause intense chemical scarification and alteration of the permeability of seed coats (Egerton-Warburton 1998) and it is possible that smoke is acting in a similar way as the environment of the gut in overcoming dormancy.

Dispersal can affect plant dynamics (Bullock *et al.* 2002) and animal seed dispersers may play an important role in maintaining regional biodiversity, in linking patches of remnant vegetation (McGrath & Bass 1999) and in increasing species-richness in restoration projects (Traba *et al.* 2003). Differences in disperser action on the seeds of plants they consume can contribute to heterogeneity of plant communities (Traveset *et al.* 2001). Being sedentary, plants cannot move across the landscape unaided. Endozoochory may confer ecological benefits by promoting substantial and dispersed seedling recruitment. For seeds that rely on endozoochory for movement across the landscape dispersal distance will be related to animal home range dimensions. The greatest distances moved by non-dispersing individual quokkas, Gilbert's potoroos and bush rats, measured by trapping at Two Peoples Bay, are 475 m, 870 m and 540 m respectively (JA Friend unpub.). Although *B. fusiformis* is widespread at Two Peoples Bay Nature Reserve, no plants were recorded adjacent to trap lines where faecal samples were collected. Further investigations would be needed to determine whether seed abundance in faecal matter is correlated with abundance of plants in the vegetation.

Seeds adapted to survive ingestion have similar properties to those adapted to survive in the soil seedbank, namely small round, hard seeds (Pakeman *et al.* 2002). Seeds that can build up in the soil seedbank can have a significant effect on species richness and abundance after disturbance events. In the colonisation of new sites or those subjected to extreme disturbance (such as extensive wildfire or volcanic eruption), vegetation dynamics may be driven by immigrant seeds where a pre-existing soil seedbank is absent or depauperate. Seeds dispersed in faeces have a ready supply of nutrients and should have a competitive advantage for germination in nutrient-poor sites. And in fire-driven environments, when fire is absent for long periods of time, endozoochory may be an important contributor to successful seed germination and establishment of plant species.

The question of whether seeds are being eaten selectively or in proportion to their availability remains unanswered, though it is unlikely that *Billardiera* is a critical food resource for these small mammals, given its relative rarity at the study site and its seasonal availability. We have not attempted to determine seasonal variation in consumption of seeds and it is possible that considerable seasonal variation, as reported by Bennett & Baxter (1989) for long-nosed potoroos, occurs. With 30 to 50 seeds per fruit, the quantity of fruit consumed by the three mammals during the sampling

period appears low. We do not know how passage through the gut has affected seed survival as we have no information about the original quantity of seeds consumed by each animal. Seeds of *B. fusiformis* are small (< 2 mg in weight) and are likely to have escaped destruction by mastication. Ingestion of *Billardiera* is more likely to be opportunistic and of more benefit to the plants themselves. When plants depend on animals for seed transport they are susceptible to dispersal failure if their seed vectors become rare or extinct (Willson 1992). Where natural regeneration is dependent on seed dissemination, failure to disperse propagules could deplete plant populations. Low seedling recruitment and even local extinction of populations may occur. Small mammal species have experienced declines or complete extinction in many parts of Western Australia due to the introduction of foxes and cats, land clearing and changed fire regimes. Their demise may contribute to changes in the balance of vegetation communities. Future investigations should address the demographic and genetic effects of seed dispersal for plant populations.

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Obituary: Professor Rex T Prider

The year 2005 saw the passing of Professor Rex T Prider, the first locally-born student of the University of Western Australia (UWA) to occupy one of its chairs. He was born at Narrogin on 22nd September 1910 and died in Perth on 6th October 2005 aged 95.

Rex Prider received his schooling at Narrogin State School and Bunbury High School, and studied geology at UWA, working in his Honours year on the geology of the Jimperding area near Toodyay. After graduation, he entered the mining industry during the great depression of the early 1930s. As a consequence, despite graduating with a double major in geology and chemistry, and first class Honours, he found himself cleaning boilers at the surface of a Kalgoorlie gold mine for fourteen shillings and tenpence (roughly $1.50) per shift. He remained for two years, having worked his way up (or down) to the position of assistant underground surveyor, where he could apply geological principles to his work. This experience was probably reflected later in his course in structural geology to UWA students, which emphasized stereographic-projection problems involving mines and the location of missing gold lodes.

In 1934 Rex Prider joined UWA as an assistant lecturer in geology, and three years later, having gained a Hackett Studentship, he began work at Cambridge for his PhD under Professor C. E. Tilley. His Cambridge work on the Western Australian potassium-rich intrusive rocks known as leucite lamproites laid the foundation of an international reputation in petrology. The Cambridge episode, however, left his strong Australian accent intact. He returned to become lecturer at UWA in 1939, and supervised numerous Honours projects in the Darling Range area and elsewhere in WA. In 1949 he succeeded E. de C. Clarke as Professor of Geology and Head of the Department, holding the position until 1975.

Professor Prider was co-author of two elementary geological texts, edited a book on mining in Western Australia, and published 38 papers in peer-assessed scientific journals. Much of his research was on Precambrian rocks in the Yilgarn Craton, but he was probably best known for his work on the leucite lamproites of the Kimberley region which he had begun in Cambridge. His 1960 paper in the *Journal of the Geological Society of Australia* emphasized the remarkable similarity of the lamproites in chemistry and mode of formation to kimberlites, then the only known igneous hosts of diamonds. The paper thus implied the possibility of economic diamond occurrences in the Kimberley region, and served as an impetus to exploration, leading eventually to the remarkable success at Argyle.

Professor Prider was a strong supporter of Australian scientific societies and institutes, and always encouraged students to join them. He served twice as President of the Royal Society of Western Australia (1944–1945 and 1959–60) and was awarded the Society's medal for research in 1970. He also became President of the Geological Society of Australia (1958–59), and Federal President of the Gemmological Association of Australia (1967–70). He was commemorated by colleagues who applied his name to the new mineral priderite, an accessory in leucite-

Professor Rex T. Prider, photographed at about the time of his appointment to the Chair.

bearing rocks represented by the formula $(K,Ba)(Ti, Fe^{3+})_8O_{16}$ and to the Cretaceous fossil *Anomia prideri*.

The Professor held that all geologists need a sound background in field geology, and almost until the end of his career he personally supervised many student field camps, which were notable for their lack of frills. Students were judged not only by their examination results but by their response to his spartan field programmes held under canvas in all weathers. The students of course, were able to observe him under the same conditions, and there developed a body of legend, partly true, in which he was the central figure. He went out of his way to know the students personally, and to encourage them, but when necessary he would review their efforts with pungent colloquialisms. The student reaction to all this was clear. When donations were sought from past students to establish a Rex T. Prider gold medal for annual presentation to outstanding Honours students after his retirement, there was a widespread and enthusiastic response.
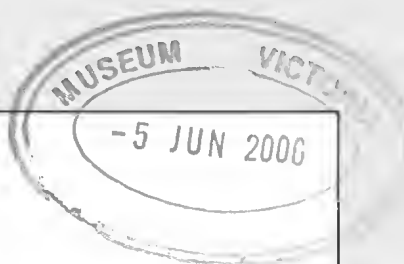
Rex Prider married Catherine Esther Walton, whom he met in Kalgoorlie, in 1936 and they had two children, son Rodney and daughter Bobbie. Sadly, he was predeceased by Rodney, an outstanding classics scholar, and shortly after in 2000, by Mrs Prider. Late in his life, in 2004, he was awarded the Chancellor's Medal of the University of Western Australia. It was presented partly in recognition of the personal efforts that he and Mrs Prider had made to enable Asian students to integrate successfully into University life, and reminds us of one of the many sides of his character.

Dr J E Glover
School of Earth & Geographical Sciences
The University of Western Australia

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Patterns of diet and microhabitat use by four species of sympatric *Ctenotus* lizards: do they reveal foraging specialisation?

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Abstract

The foraging ecology of many *Ctenotus* species is considered to be generalised and opportunistic. If their foraging ecology is generalised, we would predict that *Ctenotus* species in spinifex grasslands of arid Australia will (1) feed largely on the most abundant food source, termites and (2) that any differences in diet will largely reflect differences in microhabitat use. To test these predictions, we examined diets and patterns of microhabitat use by four sympatric *Ctenotus* species in the southern Goldfields of Western Australia. Neither prediction was supported by our results. One species, *C. brooksi*, did not feed on termites and similarity in microhabitat use between species was not related to dietary similarity. Our data suggest that these *Ctenotus* species may have more specialised foraging ecologies than has been previously appreciated. Future research involving detailed observations of *Ctenotus* species foraging in the field is required to determine which species have specialised foraging ecologies and to what extent they are specialised.

Keywords: *Ctenotus*, specialised foraging, diet, microhabitat, Goldfields, Western Australia.

Introduction

Ctenotus is the largest genus of skinks in Australia, with over 90 described species (Wilson & Knowles 1988; Cogger 2000), and is particularly diverse in spinifex (*Triodia* and *Plectrachne* spp.) grasslands of the arid zone where up to 7 species occur in ecological syntopy (Pianka 1969a). *Ctenotus* species are very difficult to observe in spinifex grasslands as they move rapidly and frequently hide in spinifex clumps, so most ecological studies have been based on dead or pit-trapped specimens (Pianka 1969b, James 1991a,b,c; Read 1998). Consequently, very little is known about the foraging strategies of *Ctenotus* species that occur in spinifex grasslands, although most studies have considered them to be generalist, unspecialised foragers (Pianka 1969a; James 1991a; Read 1998). Most ecological studies of *Ctenotus* in spinifex grasslands have reported that they feed primarily on termites (Pianka 1969b, 1986; James 1991a; Twigg *et al.* 1996; Read 1998), and this is interpreted to reflect the abundance of termites in their habitat, rather than specialised foraging strategies for termites (Morton & James 1988; James 1991a). Further, Pianka (1969b) considered the generalised foraging ecology of *Ctenotus* meant that differences in microhabitat use would result in the exposure to different prey items, so dietary differences between species would reflect differences in microhabitat use.

We examined the hypothesis that *Ctenotus* species were generalised foragers by examining microhabitat use and diet of four sympatric *Ctenotus* species in spinifex grasslands in the southern Goldfields of Western Australia. We tested the following predictions: (1) each

Ctenotus species would feed on the most abundant food source, termites, and (2) that *Ctenotus* species with the greatest similarity in microhabitat use would have the most similar diets.

Methods

Site description

The study area, centred about 18 km NE of Bungalbin Hill (30°17'S, 119°50'E) in the southern Goldfields of Western Australia, was located on a sandplain and soils throughout the study area were deep sands derived from granites. The habitat in the area was predominantly *Eucalyptus leptopoda* Mallee (JK 35), with scattered patches of *Banksia elderiana* Tall Shrubland (JK 39). The predominant ground cover in both habitats was *Triodia scariosa*. The habitat codes (JK) above are from Dell *et al.* (1988), which provides more detailed descriptions of these habitats.

Dietary intake

Individuals were captured in pit-traps in September 1992, killed with a 0.2 ml dose of 300 mg ml^{-1} of Valabarb, and their stomachs removed. Five *C. atlas*, six *C. brooksi*, six *C. schomburgkii* and 12 *C. xenopleura* stomachs were examined. The volume of each stomach was estimated to the nearest 5 µL using volumetric displacement. Stomach contents were identified to order, except for ants, which were identified to family. The number of each prey type was counted and the volumetric proportion of each prey type in the stomach was visually estimated to the nearest percent. Due to the different volume and number of prey items in the stomachs, all data were standardised as a proportion per stomach before analysis.

Microhabitat use

Microhabitat use was determined by locating individuals foraging in the study area in September 1992 and following them for up to an hour (mean = 21.2 ± 2.3 min). Five *C. atlas*, six *C. brooksi*, six *C. schomburgkii* and 15 *C. xenopleura* were followed and the average period of observation for each individual (mean ± s.e.) was: *C. atlas* (30.1 ± 10.1 min), *C. brooksi* (20.3 ± 5.0 min), *C. schomburgkii* (11.1 ± 3.3 min) and *C. xenopleura* (22.8 ± 2.3 min). Microhabitat use was divided among four categories: Spinifex (within clumps of *Triodia scariosa* or underneath overhanging foliage), Grass (within clumps of other Poaceae, Cyperaceae and Restionaceae or underneath overhanging foliage), Bush (within two cm of trunk of other plants or underneath overhanging foliage if it was within five cm of the ground) and Open (areas other than the above). The amount of time spent in each microhabitat was rounded to the nearest five sec and standardised to a proportion per lizard before analysis. The order in which each species was observed was randomised with respect to time of day (Table 1) and there was no significant difference between the species in the mean air temperature during observations ($F_{3,21}$ = 1.01, P = 0.408) (Table 1).

Statistical analysis

To determine if there were significant differences in the overall diet and microhabitat use of the four species, we analysed all variables from each class using MANOVA. For individual variables, we analysed species differences using a one-way ANOVA and conducted post-hoc analyses using a Tukey-Kramer HSD as recommended by Day & Quinn (1989). These analyses were conducted using SuperANOVA Version 1.11 (Abacus Concepts 1993). To determine whether there was a relationship between diet and microhabitat use of the four species, we calculated the similarity in each between all pairs of species using Pianka's Index (Pianka 1973). We compared similarity values for each species pair by correlation using JMP 3.2.1 (SAS 1997).

Results

Dietary intake

The proportional volume of prey consumed differed significantly between the four species (MANOVA: $F_{27,57}$ = 2.97, P = 0.001) (Table 2). The main dietary difference was in the volume of Isoptera consumed by the four species. *C. xenopleura* consumed a significantly greater volume of Isoptera than the other three species, which did not consume significantly different volumes from each other. There were also significant differences in the volume of Araneae consumed, with *C. brooksi* consuming more than *C. schomburgkii* (P < 0.05) and *C. xenopleura* (P < 0.05). *C. brooksi* also consumed more Neuroptera than *C. xenopleura* (P < 0.05). The volume of the other prey items consumed did not differ significantly between the four species (Table 2).

The differences in diet were similar when the proportional number of prey items was analysed (MANOVA: $F_{27,57}$ = 2.37, P = 0.003) (Table 3). The number of Isoptera consumed differed between all four species (P < 0.05). In addition, *C. brooksi* ate significantly more Araneae and Neuroptera than the other three species (P < 0.05). No other means were significantly different (Table 3).

Microhabitat use

Microhabitat use differed significantly between the four species (MANOVA: $F_{9,84}$ = 2.25, P = 0.026). Univariate analyses revealed that there were significant differences between species in the proportion of time spent in the Open ($F_{3,28}$ = 6.75, P = 0.001) and Spinifex ($F_{3,28}$ = 5.35, P = 0.005), but not in Grass ($F_{3,28}$ = 1.16, P = 0.343) or Bush ($F_{3,28}$ = 0.83, P = 0.487) (Fig. 1). Both *C. brooksi* and *C.*

Table 1

Range of time of day and range and mean ± s.e. air shade temperatures during microhabitat observations for each *Ctenotus* species.

Species	Time of day Range	Air temperature Range	Mean ± s.e.
C. atlas	1043 –1527	21.5 – 30.5	25.3 ± 1.6
C. brooksi	1145 –1437	24.0 – 28.0	25.8 ± 1.4
C. schomburgkii	1044 – 1557	24.0 – 29.5	26.3 ± 1.4
C. xenopleura	1032 – 1634	16.0 – 28.0[a]	23.3 ± 1.3[a]

[a] n = 8

Table 2

Proportional dietary intake, by volume, for the four *Ctenotus* species. *P*-values are for univariate ANOVAs on individual prey groups. Volumes of prey items that are not significantly different are signified by the same superscript letter.

	Species				
Prey taxa	*C. atlas*	*C. brooksi*	*C. schomburgkii*	*C. xenopleura*	*P* of $F_{3,25}$
Isoptera	0.124[a]	0[a]	0.378[a]	0.788[b]	<0.001
Formicidae	0	0.008	0.005	0.060	0.382
Coleoptera	0.126	0.073	0.258	0.011	0.145
Araneae	0.160[ab]	0.452[a]	0.03[b]	0.001[b]	0.001
Hymenoptera	0.420	0	0.325	0.067	0.089
Orthoptera	0.110	0.033	0	0	0.253
Lepidoptera	0	0.167	0	0.073	0.511
Blattodea	0.060	0	0	0	0.188
Neuroptera	0[ab]	0.267[a]	0[ab]	0[b]	0.035

Table 3

Proportional dietary intake, by number of individuals, for the four *Ctenotus* species. *P*-values are for univariate ANOVAs on individual prey groups. The numbers of Isoptera, Araneae and Neuroptera consumed differed significantly between the four species. Numbers of prey items that are not significantly different are signified by the same superscript letter.

| Prey taxa | Species | | | | P of $F_{3,25}$ |
	C. atlas	C. brooksi	C. schomburgkii	C. xenopleura	
Isoptera	0.401[a]	0[b]	0.708[c]	0.888[d]	<0.001
Formicidae	0	0.042	0.027	0.038	0.773
Coleoptera	0.135	0.098	0.071	0.018	0.166
Araneae	0.080[a]	0.390[b]	0.030[a]	0.001[a]	0.001
Hymenoptera	0.307	0	0.167	0.042	0.208
Orthoptera	0.029	0.042	0	0	0.361
Lepidoptera	0	0.167	0	0.012	0.119
Blattodea	0.100	0	0	0	0.188
Neuroptera	0[a]	0.260[b]	0[a]	0[a]	0.010

Table 4

Similarity between the volume of prey taxa consumed and microhabitat use for each species pair of *Ctenotus*, calculated using Pianka's Index. The rank of the similarities between each species pair is shown in brackets to the right of the value.

Species pair	Diet	Microhabitat
C. atlas vs C. brooksi	0.307 (4)	0.535 (6)
C. atlas vs C. schomburgkii	0.788 (1)	0.679 (4)
C. atlas vs C. xenopleura	0.459 (3)	0.991 (1)
C. brooksi vs C. schomburgkii	0.109 (5)	0.981 (2)
C. brooksi vs C. xenopleura	0.033 (6)	0.575 (5)
C. schomburgkii vs C. xenopleura	0.721 (2)	0.713 (3)

schomburgkii spent significantly more time in the Open than either *C. atlas* or *C. xenopleura* ($P < 0.05$). *C. brooksi* spent significantly less time in Spinifex than *C. atlas* and *C. xenopleura* ($P < 0.05$). *C. schomburgkii* spent significantly less time in Spinifex than *C. xenopleura* ($P < 0.05$). No other means were significantly different.

Relationships between diet and microhabitat use

There were differences in both diet and microhabitat use between the species. *C. brooksi* was different from *C. atlas* and *C. xenopleura* in both diet and microhabitat use, while the last two were similar to each other (Table 4). There was no significant relationship between similarity in diet and similarity in microhabitat use (r_4 = -0.03, P = 0.960).

Discussion

Despite differences between the four *Ctenotus* species in diet and microhabitat use, there was no obvious pattern to these differences between the species. Our prediction that *Ctenotus* species, being generalist foragers, would feed primarily on termites was only partially supported. *C. schomburgkii* and *C. xenopleura* did feed primarily on termites, but they were only one of the wide variety of items consumed by *C. atlas* for which they were ranked only fourth in terms of volume, although they were the most important taxa in terms of

Figure 1. The proportion of time spent by each species of *Ctenotus* in the four microhabitats. *C. brooksi* and *C. schomburgkii* spent most of their time in the open while *C. atlas* and *C. xenopleura* spent most of their time in spinifex.

number of individuals. *C. brooksi* consumed no termites at all. These data need to be interpreted with caution as they were collected from one site at one time period, and lizards' diets are known to vary both spatially and temporally (James 1991a; Vitt & Colli 1994; Gadsden-Esparza and Palacios-Orona 1997; Vitt *et al.* 1998). The low volume of termites in the diet of *C. atlas* and the absence of termites in the diet of *C. brooksi* might be a reflection of when the study was conducted (cf. James 1991a), as the winter of 1992 was very wet. However, the dietary information for both these species is very similar to other studies conducted on these species at other sites over a range of wet and dry periods (Pianka 1969b, 1986), suggesting that the low volume of termites consumed by these species is not an artefact of the sampling period.

Microhabitat use appeared to reflect taxonomic relatedness, being most similar between the two species in the *C. schomburgkii* group (*C. brooksi* and *C. schomburgkii*) and the two species in the *C. atlas* group (*C. atlas* and *C. xenopleura*). The prediction that species with the greatest similarity in microhabitat use would show the greatest similarity in diet was not supported by our data. The main difference in diet was between *C. brooksi* and the other three species, with smaller differences recorded between *C. atlas*, *C. schomburgkii* and *C. xenopleura*. *C. schomburgkii* and *C. brooksi* had similar microhabitat preferences but consumed very different prey items, even though they are of similar size (Pianka 1969b; MDC, unpublished data). *C. atlas* and *C. xenopleura* also had very similar microhabitat preferences but had different diets. One possibility for the lack of concordance between diet and microhabitat use maybe that animals ingested prey items from pit-traps. However, our dietary information for *C. atlas*, *C. brooksi* and *C. schomburgkii* are similar to data from Pianka (1986), who collected his data from free-ranging animals. In addition, if animals were eating invertebrates from pit traps then we would expect the diet of all four species to be similar, which they are not suggesting that the dietary information collected was from free-ranging individuals. Therefore, we concluded that the lack of concordance between the dietary and microhabitat data indicates that the four *Ctenotus* species are not generalists, foraging opportunistically on whatever invertebrates they encounter, but may instead be using particular foraging strategies to locate specific prey items within their preferred microhabitats.

Neither prediction, based on the assumption that *Ctenotus* species are generalist foragers, was supported by this study. Our results need to be interpreted with caution, as the descriptions of both diet and microhabitat use were based on small sample sizes. Ten is typically considered to be a sufficient sample size to accurately describe diets (Winemiller *et al.* 2001), which is greater than our sample sizes for all species except *C. xenopleura*. However, both our microhabitat and dietary data for *C. atlas*, *C. brooksi* and *C. schomburgkii* are similar to data for these species in Pianka (1986), suggesting our data are an accurate description of diet and microhabitat in the four species studied. Different *Ctenotus* species may encounter similar prey items, preferentially feeding on certain prey items and avoiding others. This is unlikely, though, as captive *C. brooksi* fed freely on termites (MDC, personal observation), so they

probably eat termites when encountering them in the field. Therefore, we concur with previous studies (Pianka 1969b; Archer *et al.* 1990; James 1991a; Read 1998) that *Ctenotus* species are not dietary specialists, but our results suggest that dietary differences between *Ctenotus* species studied here are likely to reflect different foraging strategies that result in them encountering different suites of invertebrates. Exactly how the foraging strategies might differ between species is not clear, as many *Ctenotus* species are very difficult to observe foraging in the field. Future research should concentrate on obtaining detailed information on *Ctenotus* species foraging in the field to determine to what extent species are specialised for specific prey items.

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Food choice by western grey kangaroos among plants grown at different nutrient levels

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Abstract

To test the hypothesis that plant palatability increases with increasing nutritional content, four native Western Australian plant species were treated with differing fertilizer regimes and presented to western grey kangaroos (*Macropus fuliginosus*) at Perth Zoo. Species were *Hardenbergia comptoniana, Notodanthonia caespitosa, Oxylobium lanceolatum* and *Rhodanthe chlorocephalum rosea*, all commonly browsed in the wild. Kangaroo feeding selection was based on the size of plants independent of nutrient concentrations. Feeding behaviour differed between treatment types, with longer time spent at greater fertilizer levels, which was related to larger plant size.

Keywords: Herbivore selection, kangaroo, nutrient concentration, plant morphology, feeding behaviour.

Introduction

Studies investigating the feeding behaviour of wild western grey kangaroos (*Macropus fuliginosus*) at Whiteman Park Reserve, Perth, Western Australia, revealed a strong positive selection of plants high in nitrogen, potassium and phosphorus (Rafferty *et al.* in press). Reports of selection for plants high in nutritional quality have been observed in a number of herbivore species (Braithwaite et al. 1984). The bridled nailtail wallaby (*Onychogalea fraenata*) showed a positive selection for food items of relatively high nutritional value (Dawson 1995; Evans & Jarman 1999). Similarly, Bergstrom & Berqvist (1997) noted that, for small coniferous and deciduous tree seedlings, grazing by large herbivores was more intense upon planted seedlings than naturally regenerating ones, suggesting it was the result of improved nutrient status of planted seedlings relative to the surrounding vegetation. Waring & Cobb (1992) reported that, for 67% of herbivore nutritional studies, herbivores performed better on fertilized plants, showing greater vigour and health. Tripler *et al.* (2002) showed browse rates to differ between control and fertilised plots for white-tailed deer (*Odocoileus virginianus*). Similarly, Holdo (2003) showed for the African elephant (*Loxodonta africana africana*), a strong preference for tree species occurring on more fertile soils (such as those associated with termite mounds) than those on sandy soils with lower nutrient concentrations.

It remains unclear whether herbivore selection of plants grown in high nutrient level environments is due to increased plant size, decreased plant defences, increased nutrient levels or a combination of these factors. The Plant Vigour Hypothesis (Price 1991) proposes that herbivores perform best on faster growing plants, because plant growth rate is usually correlated

with nitrogen levels, although other nutrients may also be important influences of plant palatability (Provenza *et al.* 2003).

The aim of our study was to observe changes in feeding selection of kangaroos upon four palatable native plant species grown under four varying nutrient regimes. Using captive western grey kangaroos at the Perth Zoo, behavioural facets of food selection were monitored to test the hypothesis that plants with high nutritional value are highly palatable, while this palatability declines with decreasing nutrient content. Whether kangaroos actively seek out plants of higher nutritional value, as suggested from our earlier results examining feeding of wild macropod on seedlings of 19 species at Whiteman Park Reserve, was explored here in a controlled environment (Rafferty *et al.,* in press). Whiteman Park Reserve is a conservation and leisure reserve of 3 600 hectares, located 18 km NE of Perth. The primary native herbivore species in the park are the western grey kangaroo (*Macropus fuliginosus*), the black-gloved wallaby (*M. irma*), and the introduced European rabbit (*Oryctolagus cuniculus*). Annual rainfall at the reserve averages 800 mm per year, with most received in the winter months in a typical Mediterranean trend. Vegetation ranges from low woodland to low open forest of *Banksia attenuata* – *B. menziesii* – *B. ilicifolia* on deep pale grey sands, to *Corymbia calophylla* on moister dark grey soils on flatter, lower areas, with local additional species reflecting soil moisture (*Melaleuca preissiana*) or sandier (*Banksia ilicifolia, B. menziesii*) soils. Plants species reflect the typically nutrient poor sandplain soils.

Materials and Methods

Nutrient and morphological analyses were performed upon a subset of 20 native plants endemic to the Swan Coastal Plain near Perth. These species incorporated a variety of leaf types and growth forms, and are

commonly browsed in the wild. Of these, four of moderate nutrient content were selected for the selection trial. These were *Hardenbergia comptoniana* (herbaceous climber), *Notodanthonia caespitosa* (grass), *Oxylobium lanceolatum* (herbaceous shrub), and *Rhodanthe chlorocephalum rosea* (herbaceous annual). All species were raised from seeds supplied from Nindethana Seed Service from Western Australian sources. In April 2001, seeds were sown into a 1:1 peat/sand mix. Seedlings were later transplanted when 3–5 cm high into 10 cm $\times$ 10 cm square black plastic pots. Pots were watered daily and covered with shade cloth until this was removed in June to allow seedlings to harden-off. Plants were monitored on a weekly basis following planting for signs of invertebrate damage or leaf senescence.

Plants were treated weekly after germination with 100 mL of Thrive® fertilizer, a powdered concentrate made into liquid form by addition to deionised water (27% N, 5.5% P and % K). Four treatment concentrations were used: low, one-eighth scoop to 9 L (approximately 3g) ; moderate, half scoop to 9 L (7g); high; one scoop to 9 L (15g); and very high, two level scoops to 9 L (30g). Attempts were made to use a treatment with no fertilizer addition, although the high mortality of this group led to its omission.

At six months old, plants were presented to a population of eight western grey kangaroos (*Macropus fuliginosus*) in the Australian Bushwalk at Perth Zoo, South Perth during daily visits to the enclosure over one week. Kangaroos typically fed upon pelletised feed and a range of chopped vegetables, but were acquainted with browsing native foliage on a regular basis with branches of a range of native plant species spread in the enclosure as supplementary food items.

Experimental offerings began two weeks after final fertilizer application to ensure no residual fertilizer remained on the foliage. Total leaf number and plant height were recorded prior to presentation. Ten replicates of the each species were presented, with each of the four fertilizer treatments represented in each replicate for the four species. Species were presented to kangaroos in a random arrangement to ensure they did not become acquainted to a particular plant type. Trays containing the four pots were used to assist stabilising pots in the presentation process, and they were presented to one or two kangaroos at a time, with other kangaroos discouraged from participating by accompanying volunteers. This simplified behavioural observations and mimicked natural conditions where fierce competition for small plants would typically be minimal.

Five preliminary trials were undertaken prior to experimental presentations to acquaint animals with the food source. It was decided that cessation of trials upon consumption of half of the plant material was the most suitable measure, rather than a set time interval, to ensure selection was not influenced by plant 'availability' and allow for the ability of some kangaroos to process food items at a greater rate. Times therefore varied for each presentation, as determined by kangaroo interest and rate of feeding activity. Following presentation, plant height and leaf number was again recorded. Behavioural responses and time spent feeding were collated.

Chemical and morphological analysis

Nitrogen, potassium, phosphorus, calcium, magnesium and sulfur were analysed for each of the four treatments of each species. Elements selected were analysed due to their high importance in relation to plant growth and morphology. Whole plants of each species (including leaves and stems which were all observed to be consumed in practice trials before commencement of the study) were collected on the first day of presentation, dried at 60° C for 48 hours in an air-forced oven and milled using a coffee grinder, followed by milling to < 1 mm in a cross beater mill (Culatti Pty. Ltd. Michigan, USA). Ten milled plants were bulked and stored in glass sample jars -5°C. Protocols used for each were as follows.

Nitrogen, potassium, phosphorus

For N content determination, 200 mg plant material was digested with H_2SO_4 and H_2O_2 in the presence of salicylic acid (Bradstreet 1965) and analysed using a Technicon segmented analyser with Berthelot colorimetric determination (Searle 1984). Determination of total P and K was undertaken using similar methods, although molybdate/vanadate colorimetric reaction and flame emission spectrometry (Varley 1966) were used respectively.

Calcium, magnesium and sulfur

200 mg of plant material was digested using nitric/perchloric acid in a block digestion at 200–210°C, with nitric acid addition to prevent nutrient loss due to charring. Upon cooling, the mixture was diluted with deionised water and the elements quantified using inductively coupled plasma atomic emission spectroscopy (McQuaker *et al*. 1979).

Morphological analysis

Leaf : mass area, leaf thickness and dry density were determined as described by Witkowski & Lamont (1991) for treatments, and amendment was made to the formula for leaf : mass area and density for the needle-leaved *Notodanthonia*, by dividing rather than multiplying the standard formula by 0.7854 (Witkowski & Lamont 1991). Leaf area was measured using the Dias system (Delta-T Devices, Cambridge, England). Average plant heights and biomasses were calculated for each treatment of each species by taking the average of ten plants harvested at the time of presentation.

Consumption measures

Consumption measures were dependent upon plant morphology. For all species, except *Notodanthonia*, numbers of leaves consumed were converted to volume for analysis by multiplying percentage leaf number eaten by original biomass. For *Notodanthonia*, leaf number was not representative of selection, as browsing did not always affect leaf number, thus percentage height eaten was multiplied by original biomass. As kangaroos commonly ate only the leaf tips of this species, height was considered a more reliable measure. As biomass values before and after presentation for each treatment and species were non-normal, results were analysed using one-tailed Wilcoxon signed ranks tests (SPSS 11 for Mac, 2002). Feeding times were analysed using ANOVA and Tukey's pairwise comparisons after removal of zeros

and log transformation to normalise the data (SPSS 11 for Mac, 2002). Log-likelihood contingency analyses (Zar 1999) were undertaken upon eaten/not-eaten values to indicate any significant differences in the presence of multiple zero scores for consumption and behavioural measures.

Results

Plant morphology and chemistry

Plant attributes (percentage eaten, height, leaf area, leaf thickness, leaf density, LMA, N, P, K, Ca, Mg and S) for each species at each application level are provided in Table 1. Of all attributes, plant height (Table 1) and biomass (Fig. 1) had the greatest variation between treatments, with greater fertilizer application resulting in increased plant size for all species, although for three species, the highest level of nutrient addition resulted in reduced total biomass (supra-optimal nutrient availability). Leaf nutrient content (N and P) increased with increased fertilizer application for *Rhodanthe*, while for all other species, leaf nutrient concentrations varied independently of fertilizer treatment.

Selection of treatments

Contingency analyses for numbers of plants damaged showed selection was independent of fertilizer treatment for *Hardenbergia, Oxylobium* and *Rhodanthe* (Table 2, df = 3, $P > 0.05$). Percentage of plants damaged did not differ significantly for *Hardenbergia, Oxylobium* and *Rhodanthe*. A significant difference in the number of plants damaged per treatment was noted for *Notodanthonia* (Table 2, df = 3, $P < 0.05$), with more plants in treatments 2, 3 and 4 consumed than to treatment 1. All species suffered significant loss of biomass following presentation independent of treatment, with the exception of treatment 2 for *Hardenbergia* and treatment 1 for *Oxylobium* (Fig. 1). A significant correlation between amount eaten and plant size was evident for all species combined (Fig. 2, r^2 = 90.7%, $P < 0.0001$, df = 15).

Kangaroo behaviour

Feeding times differed significantly between treatment types for all species (Fig. 3, df = 3, $P < 0.05$). Kangaroos typically fed on closest plants available on all occasions, moving to the next closest when feeding was completed or became difficult, e.g. if all easily accessible foliage was

Table 1

Mean physical and chemical attributes for shoots in the four treatments (Tt) and percentage of plants eaten (%) of the four species. Treatment 1 = 1/8 scoop of Thrive® to 9 L, 2 = 1/2 scoop, 3 = 1 scoop and 4 = 2 scoops. For all attributes, n = 10. Chemical analyses were undertaken on pooled samples. Units of measurement were as follows: height (ht) in cm, consumption: % leaves/height eaten, leaf area in mm^2, leaf thickness in mm, leaf density: mg mm^{-3}, LMA: mg mm^{-2}, N, P, K, Ca, Mg, S: % dry weight. IS: insufficient sample.

Species	Tt	% Plants eaten	Ht	Area	Leaf thickness	Density	LMA	N	P	K	Ca	Mg	S
Hardenbergia	1	27.5	10.6	478	0.3	12	36	2.56	0.13	1.30	1.01	1.09	0.40
comptoniana	2	41.9	37.1	713	0.3	16	48	2.10	0.19	0.90	0.57	0.78	0.38
	3	40.2	40.3	145	0.3	13	38	2.51	0.20	0.90	0.46	0.59	0.21
	4	62.4	35.7	772	0.3	15	45	3.65	0.43	1.17	0.37	0.58	0.43
Notodanthonia	1	19.4	2.7	6	0.2	31	120	IS	0.08	0.25	0.17	0.27	0.27
caespitosa	2	43.2	4.6	9	0.5	17	84	1.82	0.20	0.56	0.12	0.16	0.26
	3	44.6	6.5	11	0.3	19	77	1.63	0.13	0.22	0.12	0.15	0.13
	4	38.1	7.1	19	0.2	31	93	2.17	0.22	0.24	0.12	0.17	0.18
Oxylobium	1	33.3	12.0	234	0.3	12	46	2.23	0.14	0.69	0.28	0.51	0.26
lanceolatum	2	42.4	21.9	402	0.2	18	55	3.14	0.40	0.85	0.16	0.30	0.22
	3	31.1	34.2	338	0.2	18	52	1.67	0.018	0.88	0.19	0.33	0.16
	4	45.6	23.4	707	0.2	19	56	2.14	0.44	0.81	0.14	0.31	0.18
Rhodanthec	1	25.7	13.1	25	0.3	26	63	2.40	0.20	1.23	0.83	0.42	0.31
hlorocephalum	2	65.9	14.8	23	0.3	20	56	2.98	0.35	1.51	0.78	0.56	0.40
rosea	3	63.4	13.2	33.2	0.3	18	53	4.79	0.95	2.29	0.54	0.33	0.49
	4	42.7	22.2	25.2	0.3	7	19	4.80	0.93	2.11	0.37	0.27	0.46

Table 2

χ^2 contingency data for the number of plants damaged for each species presentation (n = 10), E = eaten, N = non-eaten. Significance determined using log likelihood analysis, df = 3 for all species.

Treatment	1 E	1 N	2 E	2 N	3 E	3 N	4 E	4 N
Hardenbergia comptoniana	4	6	8	2	6	4	9	1
Notodanthonia caespitosa	3	7	8	2	9	1	8	2
Oxylobium lanceolatum	5	5	8	2	6	4	8	2
Rhodanthe chlorocephalum	4	6	9	1	8	2	6	4
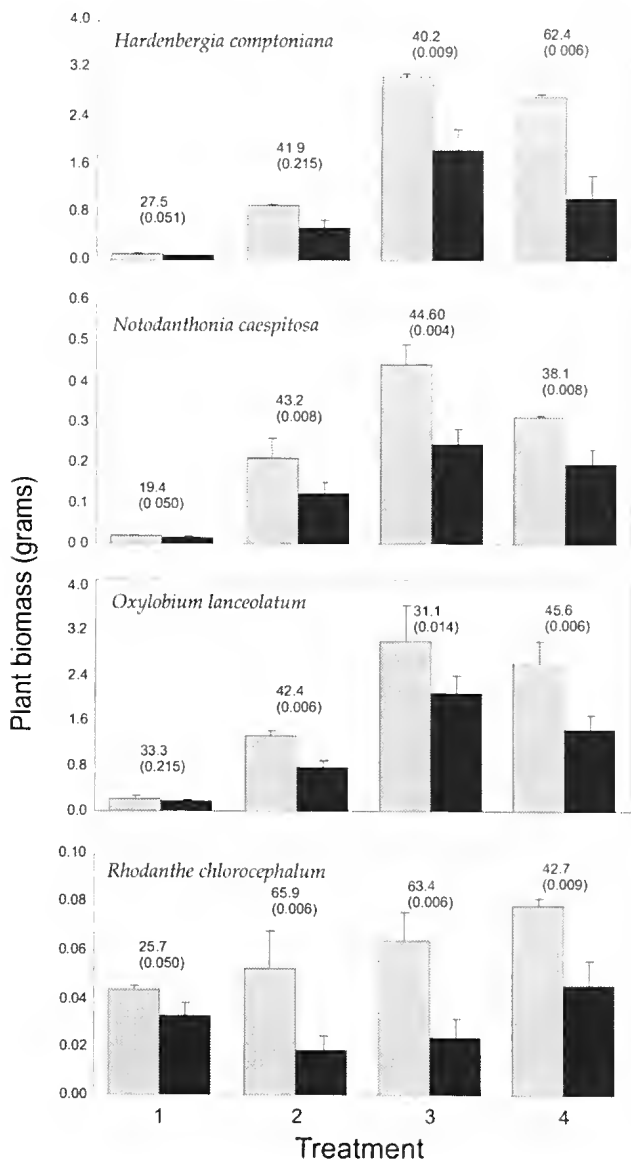
Figure 1. Biomass of plants before (light grey) and after (dark grey) presentation. Percentage biomass of plants consumed for each treatment type provided above standard error bars (fertiliser application: 1 = low, 2 = moderate, 3 = high, 4 = very high). P values (in brackets) denote differences between plant biomass before and after presentation.

removed. This trend was only interrupted with the participating of a second kangaroo, in which case the second animal selected the closest accessible after consideration of the initial feeding kangaroo. A significant correlation between time spent eating and plant size was evident (Fig. 4, r^2 = 68.4%, df = 15, P < 0.0001).

Discussion

In a captive setting at Perth Zoo, it appeared plant selection by western grey kangaroos was independent of plant morphology. The extent of plant browsing was similar to the number of plants browsed and the initial size of plants, with kangaroos appearing to eat what was
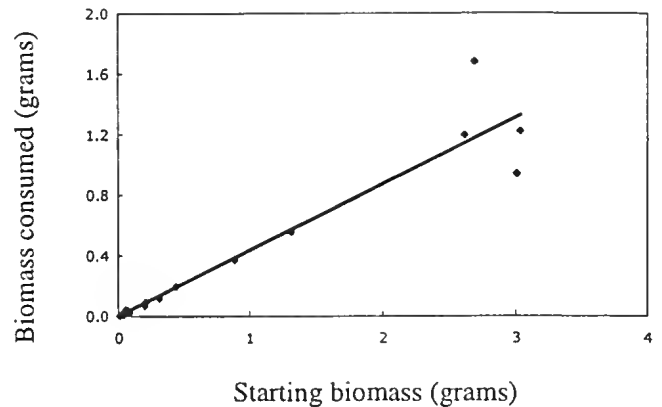
Figure 2. Relationship between starting biomass of plants with biomass consumed for all species.
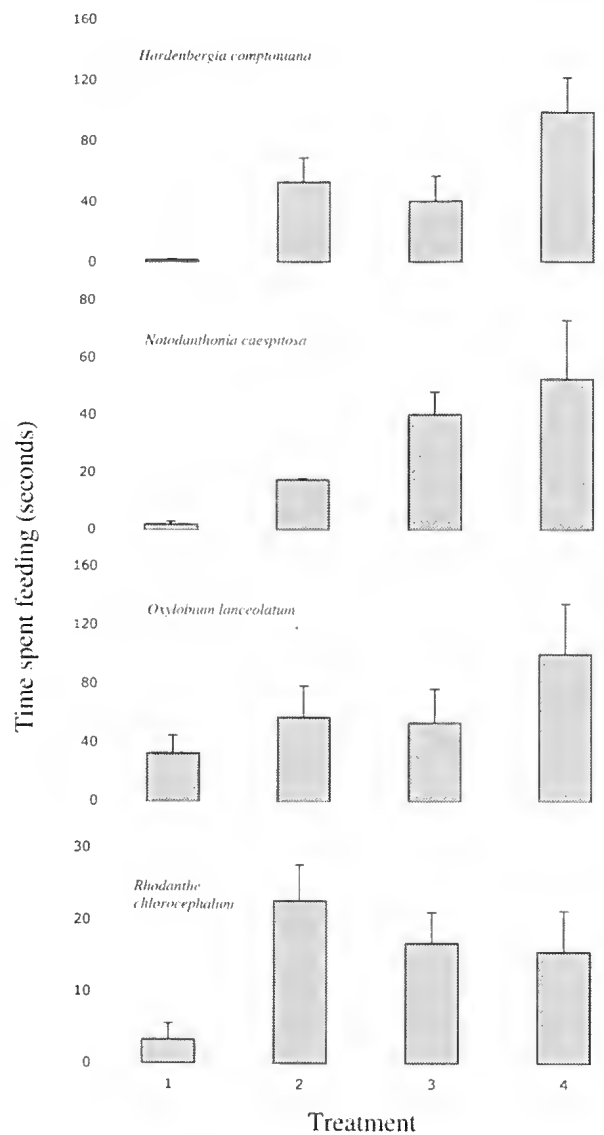
Figure 3. Total time spent feeding upon different treatments (fertilizer application: 1 = low, 2 = moderate, 3 = high, 4 = very high) for a. *Hardenbergia comptoniana*, b. *Notodanthonia caespitosa*, c. *Oxylobium lanceolatum* and d. *Rhodanthe chlorocephalum* (bars denote standard errors).
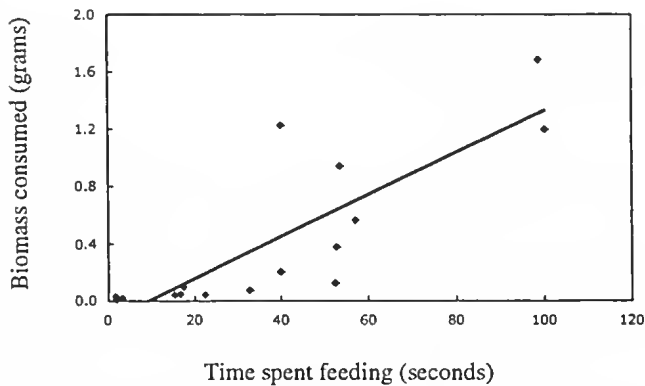
Figure 4. Relationship between starting biomass of plants and time spent feeding for all species.

proportionally available. Once a plant was initially tasted, kangaroos usually continued feeding until foliage was significantly reduced or removed entirely. This was confirmed by time spent feeding and amount consumed. It is difficult to base selection patterns upon plant nutrient concentration however, with concentrations increasing with increased fertilizer application for only one species, despite most plants growing larger with increased fertilizer application. Abrahamson & Caswell (1982) showed that the abundance of most nutrients in the soil showed no correlation with the concentration of that element in shoots. Nutrient application may therefore alter plant morphology but not necessarily nutrient concentration. Thus it is not surprising kangaroos did not select plants on the basis of their nutrient concentrations. The lack of association between nutrient content and selection may also be influenced by the expected satiated nutrient status of captive kangaroos. Animals participating may not ever have been required to base their selection upon nutrient requirement, having unlimited access to a constant, balanced diet. A captive population was selected over presentation in a wild setting, allowing for greater control of conditions and close behavioural observation. While a zoo environment is unnatural in many ways, Bourke (1989) found macropod behaviour was not seriously affected by captivity. Use of plants in the field is difficult as some groups may be eaten in the first night of presentation while others in close proximity may remain untouched for up to six weeks.

Treatments with greater fertilizer applications (i.e. 3 and 4) plants grew faster and larger. According to the Plant Vigour Hypothesis (Price 1991) herbivores perform best on faster growing plants, with growth rate often correlated with high nitrogen. While plants receiving greater fertilizer concentrations were larger, kangaroo selection on this basis was not evident. Belovsky et al. (1991) suggest that food selection is not typically based upon protein content of foliage, which is generally well above that thought to be limiting herbivore nutrition, regardless of habitat. Wright et al. (2004) reported that at the world level, there appears to be an important relationship between leaf nutrients, particularly N and P, and LMA. They suggest food selection is based on foliage texture rather than chemical content, although in the present study, it appears kangaroos simply ate what was

proportionally available, i.e. consuming greater amounts of highly fertilised plants simply due to their greater biomass. With the exception of *Notodanthonia*, kangaroos were always observed to feed upon the closest, most convenient plants for most presentations, suggesting feeding convenience was the driving factor for observed selection patterns, at least in a captive setting. Whether kangaroos in a natural environment would exhibit similar behaviours is difficult to quantify, and controlling for the great number of environmental effects difficult to achieve. Seasonal influences in the wild may also be highly influential, with selectivity often influenced by the abundance of alternative food sources (Atsatt & O'Dowd 1976; Marten 1978). Nutrient content of plants may be irrelevant in summer months when alternatives are scarce and any food item welcome, while in the winter and spring, when abundant pasture land is available for grazing for many kangaroo populations, nutritional content of food items may be equally irrelevant (Murden & Risenhoover 1993).

While it may be true that risk of herbivore damage is maximal on plants growing in nutrient-rich soils (Gowda et al. 2003), it is more likely to be a large-scale, overall effect than one of individual plant nutrient content as tested in this study. Concentration of feeding activity by herbivores in regions of high-fertility would undoubtedly provide benefits to herbivores. Plants typically show greater biomass production in these environments; thus it is sensible that herbivores should focus feeding activities in areas of high production where possible (Stephens & Krebs 1986). Individual plants growing in highly fertile substrates may be positively selected for, with risks of damage increased by greater, more prolific growth. It is unlikely, however, that individuals growing nearby in less fertile microsites, would be selected against on the basis of nutrient content given the typically limited nature of forage, particularly in warmer months when wild kangaroos appear to target any suitable food item. While plants grown in less fertile areas may be smaller and less conspicuous, escaping attention to a greater extent than their more fertile counterparts, it is likely they too would be eaten by kangaroos if intercepted while foraging. Visual cues, in conjunction with feeding convenience, may therefore be more important than nutritional content, particularly in forage-limited environments.

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The Bunjil L6(S4) ordinary chondrite, a new meteorite find from Western Australia

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Abstract

A broken, orientated, stony meteorite mass weighing 38.75 kg was found in 1971 at a locality (29° 37' 45"S, 116° 28' 56"E) near Bunjil in the northern wheatbelt of Western Australia. The presence of relict chondrules and the mean compositions of the ferro-magnesian silicates (olivine $Fa_{25.1}$; orthopyroxene $Fs_{21.4}$) show that the meteorite belongs to the L-group of ordinary chondrites. The strongly recrystallized chondritic texture and the presence of large (> 50 μm) crystals of plagioclase feldspar (now partially converted to maskelynite) show that the meteorite belongs to petrologic type 6. Olivine containing abundant planar fractures and displaying incipient mosaicism, together with plagioclase partially altered (< 75%) to isotropic glass with variable compositions, and the presence of shock-veins, indicate that the meteorite has been subjected to shock-loading appropriate to stage 4 (approximately 30 kb shock pressure). Bunjil is very similar to the previously described Latham (L6) ordinary chondrite reportedly found nearby, and the two meteorites may belong to the same fall.

Keywords: meteorite, chondrite, Bunjil, Western Australia

Introduction

Prolonged aridity throughout a large area of Western Australia has provided conditions conducive to the preservation of meteorites. As a result, large numbers continue to be recovered (Bevan 1992; Bevan 1996; Bevan *et al.* 1998). The Bunjil stony meteorite was found in April or May of 1971 and subsequently, the name has been approved by the Nomenclature Committee of the Meteoritical Society (Wlotzka 1995). Following ploughing, a single, broken, flight-orientated mass weighing 38.75 kg was found by Mr Peter Just at a locality 12 km E and slightly N of Bunjil, and about 13.5 km NNE of Latham, Western Australia. The find-site of the meteorite (29° 37' 45" S, 116° 28' 56" E) lies in the Victoria District on Location No. 8898. In 1991, Mr Just deposited the entire mass of the meteorite (now registered WAM 14711) at the Western Australian Museum in Perth.

The roughly conical stone (Fig. 1a,b) measures 37 cm x 25 cm x 23 cm and represents approximately two-thirds of an orientated mass. Deep, fluted regmaglypts occur on the ablated surface of the mass, particularly towards the rear of the stone. The stone is heavily weathered, but retains vestiges of a brown fusion crust. One flat, broken, weathered surface (Fig. 1b) lacks fusion crust and represents a late stage fracture, probably post-atmospheric. At the time of discovery, Mr Just searched the area unsuccessfully for the missing portion of the stone.

Mineralogy, petrology and classification

Bunjil is a chondritic meteorite displaying occasional large chondrules (up to *ca.* 4 mm in diameter) on its crusted and broken surfaces. The meteorite is deeply weathered and the interior is stained brown with terrestrial oxy-hydroxides of iron. Intergranular veins of iron oxides locally pervade the texture of the meteorite. The state of weathering, with moderate oxidation affecting less than 60% of metal and troilite, corresponds to stage W2 of the microscopic weathering scale for the ordinary chondrites as defined by Wlotzka (1993a).

In thin section, Bunjil is thoroughly crystalline, displaying poorly defined relict chondrules set in a coarsely crystalline matrix. Electron microprobe analysis (for operating conditions see Table 1) shows that the meteorite is composed essentially of forsteritic olivine with a mean composition of $Fa_{25.1}$ (n = 10, σ = 0.53), and low-Ca orthopyroxene ($Fs_{21.4}En_{77.0}Wo_{1.6}$, n=7, σ=0.61) (Table 1).

Abundant, large (> 50 μm) grains of plagioclase feldspar with the general composition of oligoclase occur throughout the matrix. Grains of plagioclase variably show strong undulatory extinction, planar features, and partial isotropism, and are locally converted to maskelynite. Less than 75% of the grains of plagioclase have been transformed to maskelynite. Measured plagioclase compositions in the meteorite are variable within the range $An_{8.5-12.8}$, $Ab_{70.6-85.3}$, $Or_{2.0-16.4}$. Those grains of plagioclase converted to isotropic glass occur mainly in the more severely shocked portions of the meteorite. Accessory minerals recognised in the meteorite include

Table 1

Point analyses (wt %) of typical individual grains of minerals in the Bunjil ordinary chondrite

	olivine	ortho-pyroxene	chromite
SiO_2	37.7	55.1	NA
TiO_2	–	0.14	2.43
Al_2O_3	–	–	6.15
Cr_2O_3	–	0.22	57.6
V_2O_3	NA	NA	0.68
FeO*	22.9	14.3	31.0
MnO	0.35	0.40	–
MgO	38.9	28.9	2.22
CaO	–	0.83	NA
Totals	99.85	99.89	100.08
	$Fa_{25.1}$	$Fs_{21.9}$ $En_{76.5}$ $Wo_{1.6}$	$\underline{100\ Cr}$ 86.3 (Cr+Al)

* total Fe as FeO; – = not detected; NA = not analysed for.

Analytical conditions: JEOL electron microprobe; accelerating potential 20 kV; operating current 20 nA; standards employed, independently analysed minerals and pure metals. (Analyst G. Pooley).

Figure 1. a, Top view of the orientated mass of the Bunjil ordinary chondrite, and b, oblique view of the meteorite. The planar surface viewed from above in a. and obliquely in b. (front) is a fractured surface (scale bars 10 cm).

metallic FeNi (both α-kamacite and γ-taenite), troilite, chromite (see Table 1) and chlorapatite.

Throughout the stone, grains of olivine show abundant planar fractures and incipient mosaicism. Opaque, interconnecting shock veins up to 2 mm wide locally traverse the fabric of the meteorite, and there are also sporadic, apparently isolated, small (< 50 μm) pockets of melted material. Within the shock veins and melt pockets, troilite and metal have been shock-melted and occur as spherical beads and stringers.

The compositions of the ferro-magnesian silicates in the Bunjil meteorite show that it belongs to the L-group of ordinary chondrites. The crystalline nature of the stone, and the presence of abundant large crystals (50 μm) of plagioclase feldspar (now partially converted to isotropic glass), indicate that the meteorite is petrologic type 6 of the Van Schmus & Wood (1967) classification. The wollastonite content of the low-Ca orthopyroxene (1.6 mol%) is also consistent with petrologic type 6 (Scott et al. 1986).

Chromite in Bunjil is slightly higher in Cr_2O_3, Al_2O_3 and MgO, and slightly lower in FeO than the average for equilibrated L-group chondrites (Table 1). However, chromite lies within the range of compositions measured for L5-6 ordinary chondrites by Bunch et al. (1967) and Wlotzka (2005).

The overall level of shock-metamorphism exhibited by the stone is appropriate to stage 4 (S4) of the shock classification of the ordinary chondrites proposed by Stöffler et al. (1991). The variability of the plagioclase compositions is consistent with plagioclase described from other shocked ordinary chondrites of stages 4–5, and may have resulted from the mobilisation of Na during shock-loading (Rubin 1992).

Discussion and conclusions

Bunjil is an L6 ordinary chondrite that has suffered post-recrystallization shock-loading appropriate to shock pressures in the range 30–35 GPa according to the classification of Stöffler et al. (1991). However, more recently, Schmitt (2000) has calibrated experimentally the pressures required to induce similar shock features in an ordinary chondrite (Kernouvé H6). The shock recovery experiments (Schmitt 2000) indicate that these shock effects may be produced at shock pressures < 30 Gpa at a low initial temperature (293 K), and at < 25 Gpa at a high initial temperature (920 K). In the equilibrated L-group ordinary chondrites, shock stages of S3 and above are commonly observed. Many of these severely shocked meteorites display extensive blackened veins containing melted material. However, Stöffler et al. (1991) advised against the use of shock veins as the primary indicators of shock levels, since they are not representative of the overall equilibrium shock pressure experienced by the meteorite. The general condition of the olivine and plagioclase grains in such shocked meteorites is a much better indicator of equilibrium shock pressures (Stöffler et al. 1991). More recently, van der Bogert et al. (2003) have shown experimentally that severe shock deformation is not always required for the formation of melt veins and darkening in chondrites. Instead, high strain rates and frictional melting are particularly
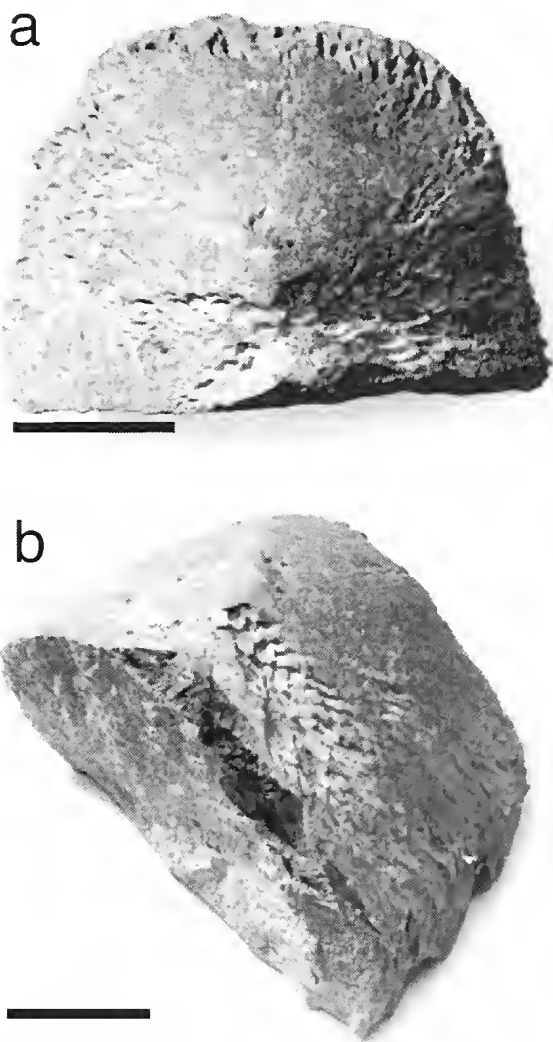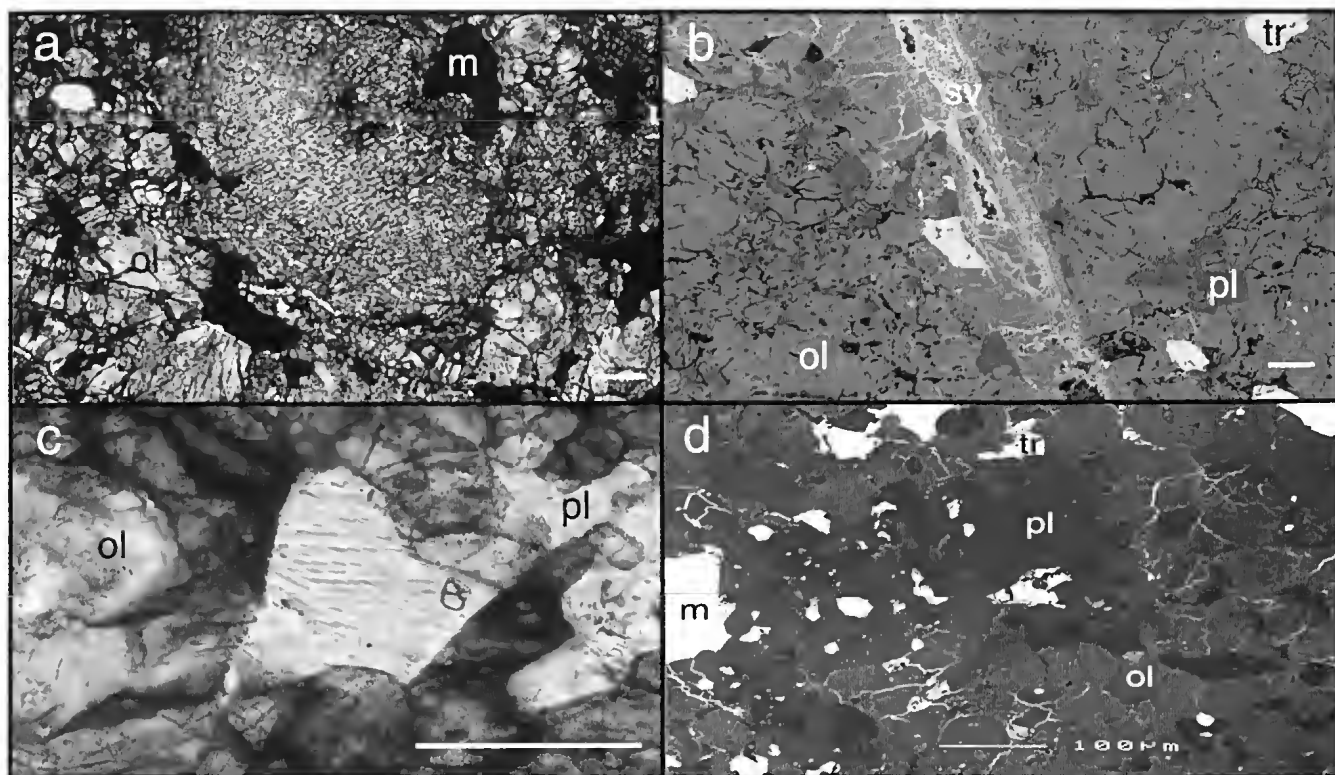
Figure 2. Photomicrographs of the Bunjil L6 ordinary chondrite in **a**. plane-polarised light (PPL) showing strongly recrystallised chondritic texture with olivine (ol). Dark patches are metal (m) and other opaques. (scale 100 µm) **b**. reflected light showing a large shock vein (sv) containing melt droplets of metal and troilite (tr) (scale 25 µm). **c**. A grain of plagioclase feldspar (centre, PPL) showing planar features as the result of shock metamorphism (scale 50 µm). **d**. Back-scattered electron image showing plagioclase (pl), olivine (ol), troilite (tr), and FeNi metal (m) (scale 100 µm).

important for the formation of veins at low shock pressures. Moreover, Rubin (2002) has suggested that the presence of "shock" veins in some apparently unshocked ordinary chondrites indicates that they suffered prolonged post-shock thermal annealing that effectively repaired the shock damage in their minerals.

In Bunjil, the pervasive, shock-damaged condition of the meteorite's constituent silicate minerals (planar fractures, planar features, incipient mosaicism, and maskelynite) do not indicate any significant post-shock annealing of the silicates. In Bunjil, then, the black veins are very likely to have been formed by shock-related frictional melting.

The planar, fractured surface on the Bunjil stone suggests that the original mass broke late in flight, or perhaps on impact. Another chondritic meteorite, Latham, found in 1977 in the same general area as the Bunjil stone is also an L6(S4) chondrite (Bevan 1992; Wlotzka 1993b) and may be a fragment of the missing portion of the Bunjil stone.

Little is known of the recovery of the Latham ordinary chondrite. A fragment of unknown weight was reportedly found in the general vicinity of Latham (29° 45' S, 116° 26' E), although the exact locality is unknown. The main fragment of the Latham meteorite remains in the possession of the finder and is unavailable for further study. However, a chip weighing 1.1 grams (registered WAM 13456), and a thin section are in the collection of the Western Australian Museum. Latham contains olivine ($Fa_{24.3}$) (incorrectly reported in Wlotzka [1993b] as $Fa_{4.3}$)

and low-Ca orthopyroxene ($Fs_{20.4}$) with ranges of compositions that overlap with those measured for these minerals in Bunjil. The Latham chondrite is also moderately to strongly shocked containing some maskelynite. A microscopic comparison between Bunjil and Latham (this work) shows that they are petrologically similar, and appear to belong to the same stage (S4) of shock alteration of the Stöffler et al. (1991) classification. There is a possibility that Latham and Bunjil are from the same fall and, pending further studies (terrestrial age and noble gases), the meteorites should be paired.

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Diatoms as ecological indicators in lakes and streams of varying salinity from the wheatbelt region of Western Australia

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Abstract

Secondary salinisation has adversely affected the water quality of lakes and streams in the wheatbelt region of Western Australia. This study involved sampling 51 waterbodies in 1999, with the aim of determining the distribution pattern of diatoms in relation to salinity. In total 72 taxa were recorded, with an inverse trend observed between species richness and salt loading. Multivariate analysis (semi-strong-hybrid multidimensional scaling) revealed that salinity was a key factor (PCC r=0.62) influencing species distribution. Diatom assemblages characteristic of different salinity regimes have been identified. For example, *Amphora coffeaeformis*, *Hantzschia baltica* and *Navicula salinicola* were commonly associated with hypersaline conditions. Diatoms proved to be useful biomonitors of salinisation, with the research presented currently being expanded to develop a predictive model for salt-affected wetlands in WA.

Keywords: diatoms, wheatbelt area, secondary salinisation, wetlands, indicators

Introduction

Secondary salinity can be attributed to land clearing followed by dryland agriculture and is considered to be a significant form of wetland degradation in the wheatbelt region of Western Australia. The fundamental cause of salinisation in WA is the replacement of perennial, native vegetation with annual crops and pastures used in agriculture (Smith & Finlayson 1988). This has allowed rainwater that was previously being used by deep-rooted plants to enter groundwater, mobilising salts stored in subsoils. As a result, water tables have risen, bringing dissolved salts to the surface producing saline seepage (Stoneman 1976; Hartley & de Vries 1983; Frost *et al.* 2001). Subsequent overland and subsurface flow of this saline water into wetlands and river systems has led to increased salinity concentrations (Schofield *et al.* 1988; Davis *et al.* 2003).

The impact of salinisation in waterbodies throughout the wheatbelt region is considered to be particularly severe, accounting for more than 70 % of Australia's salinity problem (National Land & Water Resources Audit 2001). Major catchments subjected to agricultural clearing continue to show increasing salinity trends, the rate of which is higher in low rainfall areas (Kay *et al.* 2001). In terms of salinity regimes, wetlands can be classified as freshwaters, with salinity less than 3 ppt, brackish, 3–10 ppt, saline, 10–50 ppt and hypersaline systems, with salinity greater than 50 ppt (Halse *et al.* 1993). Changes to the hydrological equilibrium as a result of salt loading adversely affect the biota of aquatic ecosystems (Stoneman 1976; Schofield *et al.* 1988). For example, Pinder *et al.* (2005) showed a negative relationship between invertebrate species richness and

salinity, and Blinn *et al.* (2004) found a similar inverse trend for diatoms from wheatbelt wetlands.

Diatoms are one of the most effective groups of organisms successfully used for biological monitoring of wetlands and rivers. They display a wide range of morphological types represented by over 900 genera (Fourtanier & Kociolek 1999), occurring in both fresh and saline environments. They are also one of the most species rich components of aquatic communities, playing a fundamental role in many food webs (Bold & Wynne 1978; Stevenson & Pan 1999).

Diatoms have a restricted distribution in relation to salinity of water, the limits of which have been extensively documented throughout the world (Compere 1994; Snoeijs 1999; Blinn & Bailey 2001). However, there has been little research on establishing the tolerance of different taxa to varying salt levels in Western Australia. Therefore the objective of this study was to gather data on the response of diatom species to salinity through sampling representative waterbodies in the wheatbelt region. A number of species indicative of varying salinity regimes were also identified, with potential applications for future biomonitoring protocols. The baseline data obtained from this research may be incorporated into a predictive model that can be used in future management strategies for lakes and streams impacted by secondary salinisation.

Methods

Sampling of 51 sites from lakes and streams in the wheatbelt region of Western Australia was carried out between January and September 1999. The GPS coordinates of the study sites (and allocated codes) are shown in Table 1, with the locations indicated on Fig. 1.
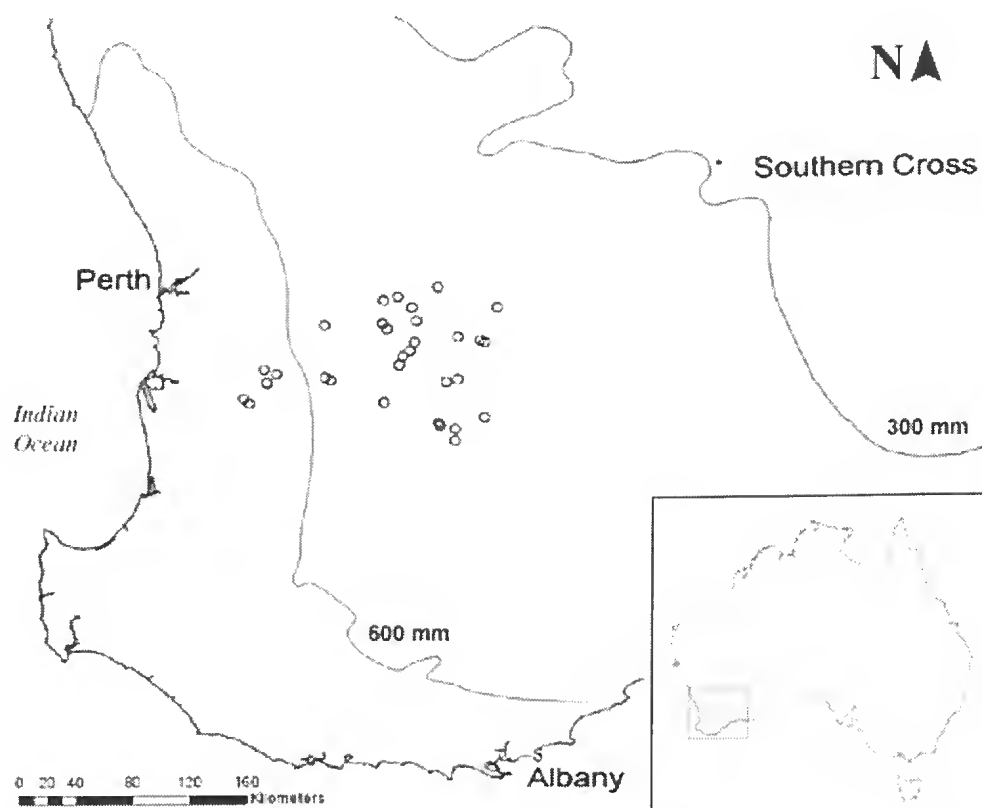
Figure 1. Location of study sites in the wheatbelt region of the south-west of Western Australia, approximately defined by the 600 mm and 300 mm annual isohyets. Sites were situated within a 250 km radius from the Perth metropolitan region.

Table 1

List of study sites and codes, where W designates wheatbelt, and number indicates order of sampling. GPS coordinates are shown for each site.

Code	Site Name	Coordinates	Code	Site Name	Coordinates
W01	Avon River: Gwambygine Pool A	32° 16.51' S – 117° 10.54' E	W27	Yenyening Lakes	32° 14.51' S – 117° 09.06' E
W02	Avon River: Gwambygine Pool B	31° 58.40' S – 116° 47.87' E	W28	Lake Mears	32° 13.61' S – 117° 21.59' E
W03	Avon River: Gwambygine Pool C	31° 59.13' S – 116° 48.26' E	W29	Yornaning Dam	32° 44.44' S – 117° 09.51' E
W04	Avon River: Gwambygine Pool D	31° 59.40' S – 116° 48.33' E	W30	Toolibin Lake Inflow	32° 54.58' S – 117° 36.57' E
W05	Avon River: Gwambygine Pool E	31° 59.51' S – 116° 48.41' E	W31	Ibis Lake	32° 59.05' S – 117° 36.57' E
W06	Avon River: Boyagarra Pool A	32° 14.51' S – 117° 09.06' E	W32	Nomans Lake	33° 00.16' S – 117° 30.30' E
W07	Avon River: Boyagarra Pool B	32° 16.51' S – 117° 10.52' E	W33	Lake Dumbleyung	33° 19.21' S – 117° 37.49' E
W08	Avon River: Mears Five Mile Pool	31° 50.11' S – 116° 48.15' E	W34	Lake Coomelberrup	33° 21.51' S – 117° 47.80' E
W09	Avon River: Suspension Bridge	31° 38.56' S – 116° 40.19' E	W35	Parkeyerring Lake	33° 21.56' S – 117° 21.17' E
W10	Avon River: Peel St Bridge	31° 38.50' S – 116° 40.19' E	W36	Lime Lake Rd West Lake	33° 24.83' S – 117° 19.38' E
W11	Avon River: Katrine Bridge	31° 36.59' S – 116° 33.11' E	W37	Norring Lake	33° 26.83' S – 117° 17.16' E
W12	Avon River: Glen Avon Pool	31° 36.52' S – 116° 32.59' E	W38	Flagstaff Lake	33° 30.22' S – 117° 15.56' E
W13	Mortlock River: Wongan Hills	31° 02.14' S – 116° 44.26' E	W39	Collie Changerup Rd Lake	33° 36.09' S – 116° 49.25' E
W14	Mortlock River: Goomalling	31° 21.02' S – 116° 45.89' E	W40	Towerrining Lake	33° 35.05' S – 116° 47.52' E
W15	Walymouring Lake Inlet	31° 08.25' S – 116° 52.56' E	W41	Williams Darkan Rd Lake	33° 14.85' S – 116° 46.93' E
W16	Lake Campion	31° 08.31' S – 118° 20.01' E	W42	Morangup Rd Dam A	31° 41.11' S – 116° 18.24' E
W17	Lake Brown	31° 04.30' S – 118° 14.51' E	W43	Morangup Rd Dam B	31° 41.12' S – 116° 18.15' E
W18	Lake Yealering	32° 35.67' S – 117° 37.61' E	W44	Morangup Rd Dam C	31° 41.18' S – 116° 18.06' E
W19	Ardath Lake	32° 05.75' S – 118° 09.37' E	W45	Toodyay Bailup Rd Lake	31° 43.58' S – 116° 16.60' E
W20	Kevills Lake A	31° 52.56' S – 117° 30.43' E	W46	Utah Rd Lake	31° 43.20' S – 116° 16.32' E
W21	Kevills Lake B	31° 53.26' S – 117° 30.77' E	W47	Toodyay Soak Well	31° 32.15' S – 116° 24.01' E
W22	Goomalling Lake A	31° 18.45' S – 116° 55.19' E	W48	Mistake Creek	31° 32.09' S – 116° 23.93' E
W23	Goomalling Lake B	31° 18.46' S – 116° 40.03' E	W49	Toodyay Rd Lake	31° 34.03' S – 116° 28.77' E
W24	Goomalling Lake C	31° 18.46' S – 116° 40.07' E	W50	Jimperding Brook	31° 37.04' S – 116° 24.94' E
W25	Goomalling Lake D	31° 18.47' S – 116° 40.02' E	W51	Bailup Rd Lake	31° 44.74' S – 116° 18.16' E
W26	Goomalling Lake E	31° 18.58' S – 116° 39.57' E			

Sites were sampled once only and included lotic and lentic waters due to the intermittent nature of aquatic systems in the area. Environmental parameters measured at each site were pH, salinity (ppt), dissolved oxygen (ppm) and temperature (°C). Water quality measurements and diatom collection were conducted from the deepest accessible point of a waterbody to provide stable sampling conditions.

An artificial substrate collector known as the JJ Periphytometer (John 1998) was placed at each site, providing a uniform surface for colonisation by diatoms from periphytic, benthic, epiphytic and planktonic habitats. This method ensured that the diatom assemblages reflected the water quality at the time of sampling. After a minimum 14-day immersion period samples were retrieved and prepared using the nitric acid digestion technique described by John (1998). Permanent slides of diatoms have been deposited at the Curtin University International Diatom Herbarium, School of Environmental Biology for future reference. Species were identified using the following specialised literature: Patrick & Reimer (1966); Patrick & Reimer (1975); Czarnecki & Blinn (1978); Foged (1978); Foged (1979) John (1983; 1998); Hustedt (1985); Ehrlich (1995); Sims (1996). A minimum of 300 diatom valves were counted and converted to a percentage frequency for statistical analyses.

The community structure of diatoms was assessed using indices including species richness and the Shannon-Wiener diversity index (Zar 1996). Multivariate statistical analysis was employed to determine the relationship between sites and environmental parameters based on diatom community structure. Ordination was carried out in PATN (Belbin 1993), using semi-strong-hybrid multidimensional scaling (SSH MDS). Correlation coefficients were generated using the principal axis correlation (PCC) routine and tested for significance with 100 Monte Carlo randomisations.

Description of Study Sites

Study sites included 28 lakes, the majority of which are intermittent, 16 sites that are tributaries or part of the Avon River system, two small inlets/inflows close to larger wetland areas and five small artificial dams.

Lentic waters comprised of a range of smaller wetlands such as Lake Coomelberrup – W34 (less than 100 ha), moderately sized lakes such as Lake Campion – W16 (approximately 600 ha) and very large wetlands such as Lake Dumbleyung – W33 (over 5500 ha) (Halse et al. 1993). Many of the waterbodies in this region have been affected by secondary salinisation, and are experiencing loss of fringing vegetation due to increasing salt loads or waterlogging (Cramer & Hobbs 2002). Drainage channels were present at some of the lentic sampling sites including Ardath Lake (W19), having the potential to impact water quality and aquatic biota (Cale et al. 2004).

The majority of the lotic sites were situated along the Avon River, or in smaller streams and tributaries. The catchment of this extensive river system covers an area of approximately 120 000 km² (Weaving 1999). Sites located further inland such as Mortlock River: Wongan Hills – W13 commonly dry out in summer months, compared to sites such as Avon River: Katrine Bridge – W11, which experiences a more consistent flow throughout the year. With over 75 % of the region cleared for agriculture the Avon has been affected by problems including salinisation, siltation and the destruction of riparian vegetation (John 1998).

Results

Water quality measurements displayed a wide variation over the sampling period. A condensed list of coded sites and corresponding pH and salinity readings is presented in Table 2. The pH of wheatbelt sites ranged

Table 2

Water quality readings of pH and salinity (ppt) from 51 coded wheatbelt sites where (*) are freshwater sites <3 ppt, (+) are brackish sites 3-10 ppt, (o) are saline sites 10-50 ppt and (^) are hypersaline sites > 50ppt. Measurements were taken between Summer and Spring 1999.

Code	pH	Salinity	Code	pH	Salinity	Code	pH	Salinity
+ W01	9.41	7.70	^ W18	7.26	96.20	^ W35	8.07	81.00
+ W02	9.40	7.70	o W19	3.99	26.30	^ W36	7.82	80.80
+ W03	9.40	7.70	^ W20	7.22	59.40	^ W37	7.92	100.30
+ W04	9.71	7.70	^ W21	6.89	68.30	^ W38	7.78	130.00
+ W05	8.90	6.70	o W22	8.44	19.80	+ W39	8.36	9.66
o W06	7.20	40.00	o W23	8.78	26.30	+ W40	8.56	5.83
o W07	7.61	18.60	+ W24	8.55	6.59	o W41	7.97	18.50
o W08	8.39	13.63	+ W25	8.14	3.64	* W42	5.88	0.21
+ W09	8.48	6.53	+ W26	7.69	5.04	* W43	6.98	0.13
+ W10	8.57	6.54	o W27	8.64	17.70	* W44	6.97	0.77
o W11	8.00	15.80	^ W28	8.67	62.60	* W45	7.97	0.76
o W12	7.71	14.60	+ W29	9.07	3.33	* W46	8.61	0.73
+ W13	8.29	6.77	^ W30	8.48	51.30	* W47	6.51	0.17
+ W14	7.15	3.84	o W31	8.06	12.52	* W48	7.97	2.52
+ W15	8.97	7.88	o W32	8.15	36.60	* W49	7.06	0.14
^ W16	6.21	73.70	^ W33	8.64	154.10	+ W50	7.82	3.20
^ W17	6.55	50.20	^ W34	5.74	87.20	* W51	7.19	1.47

Table 3

List of diatom taxa identified from wheatbelt study sites, presented in alphabetical order.

Taxa Name

Achnanthidium lanceolatum Bréb. ex Kütz.	*Diploneis subovalis* Cl.	*Nitzschia gracilis* Hantzsch
Achnanthidium minutissimum (Kütz.) Czarn.	*Entomoneis alata* Kütz.	*Nitzschia hummii* Hust.
Achnanthidium oblongella Oestrup	*Entomoneis tenuistriata* John	*Nitzschia linearis* W.Smith
Achnanthidium reidensis Foged	*Eunotia curvata* (Kütz.) Lagerstedt.	*Nitzschia obtusa* var. *scalpelliformis* Grun.
Amphora acutiuscula Kütz.	*Eunotia pectinalis* (O.F. Müller) Rabh.	*Nitzschia palea* (Kütz.) W.Smith
Amphora australiensis John	*Fallacia pygmeae* (Kütz.) Mann	*Nitzschia pusilla* Grun.
Amphora coffeaeformis (Ag.) Kütz.	*Gomphonema parvulum* (Kütz.) Kütz.	*Nitzschia sigma* (Kütz.) W.Smith
Amphora holsatica Hust.	*Gyrosigma kutzingii* (Grun.) Cl.	*Pinnularia lata* (Bréb.) W.Smith
Amphora mexicana A. Schmidt.	*Hantzschia baltica* Simon.	*Pleurosigma elongatum* W.Smith
Amphora montana Kütz.	*Mastogloia braunii* Grun.	*Pleurosigma salinarum* Grun.
Amphora turgida Hust.	*Mastogloia halophila* John	*Rhaphoneis surirella* (Ehr.) Grun. *ex* V.H.
Amphora veneta Kütz.	*Mastogloia pumila* (Grun.) Cl.	*Rhopalodia gibberula* (Ehr.) O.F.Müller
Amphora ventricosa Greg.	*Mastogloia smithii* Thwaites.	*Rhopalodia gibberula* var. *globosa* Hust.
Bacillaria paxillifer (O.F. Müller) Hendey	*Navicula auriculata* Hust.	*Rhopalodia musculus* (Kütz.) O.Müller
Brachysira aponina Kütz.	*Navicula cryptocephala* (Kütz.)	*Stauroneis dubitabilis* Hust.
Camphylodiscus clypeus Ehr. var. *bicostata* (W.Smith) Hust.	*Navicula elegans* W.Smith	*Stauroneis pachycephala* Cl.
Cocconeis placentula (Ehr.) Hust.	*Navicula ramosissima* (Ag.) Cl.	*Stauroneis spicula* Hickie
Cocconeis placentula var. *euglypta* (Ehr.) Cl.	*Navicula salinarum* Grun.	*Surirella ovalis* Bréb.
Ctenophora pulchella (Ralfs ex Kütz.) Williams & Round	*Navicula salinicola* Hust.	*Synedra acus* Kütz.
Cyclotella atomus Hust.	*Navicula subrhynocephala* Hust.	*Synedra rumpens* Kütz. var. *scotica* Grun.
Cyclotella meneghiniana Kütz.	*Navicula tripunctata* (O.F. Müller) Bory.	*Synedra ulna* (Nitzsch) Ehr.
Cyclotella striata (Kütz.) Grun.	*Nitzschia acicularis* (Kütz.) W.Smith	*Tabularia tabulata* (Ag.) Snoeijs
Cymbella minuta Hilse ex Rabh.	*Nitzschia amphibia* Grun.	*Thalassiosira weissflogii* (Grun.) Fryxell & Hasle
Cymbella pusilla Grun.	*Nitzschia fasciculata* Grun.	*Tryblionella hungarica* Grun.

from acidic (3.99) to alkaline (9.71), and salinity from fresh (0.12 ppt) to hypersaline (154.10 ppt). Dissolved oxygen varied from near anoxic (0.11ppm) to well oxygenated (13.62 ppm) and a temperature range of 10.0 °C to 24.7 °C was recorded.

The diatom taxa identified were diverse with over 70 species representing 27 genera (Table 3). The species richness recorded from each site is presented in Table 4 and the number of sites in which these species occurred is shown in Appendix 1. An inverse relationship was apparent with species richness being highest in freshwater and brackish sites (Fig. 2a). Once the salinity concentration reached approximately 40 ppt, species numbers were limited to less than 10. The results of the Shannon-Wiener diversity index also displayed a similar trend (Fig. 2b). Species richness and diversity were also related to pH (Fig. 2c & 2d), with the maximum number of species occurring when pH was close to neutral. There appeared to be no relationship between these indices and the environmental variables of dissolved oxygen and temperature.

Correlation coefficients derived from the ordination determined that salinity and pH were the two most important variables (PCC r=0.62 and 0.52 respectively), followed by dissolved oxygen (PCC r=0.36) and temperature (PCC r=0.36). The SSH biplot was generated using the statistically significant (P<0.5) variable of salinity, which was subsequently superimposed onto the ordination (Fig. 3). A clear gradient was evident with the separation of freshwater sites (<3 ppt) and hypersaline sites (>50 ppt). In comparison, some overlap was apparent between the brackish (3–10 ppt) and saline sites (10–50 ppt).

Correlation coefficients for the most common diatom species related to the wetland sites were also calculated. Nine species were shown to have statistically significant (P<0.05) correlation coefficients of greater than 0.6, which were then superimposed onto the SSH biplot (Fig. 4). *Achnanthidium minutissimum* (PCC r=0.79), *Synedra rumpens* var. *scotica* (PCC r=0.61) and *Gomphonema parvulum* (PCC r=0.71) were highly correlated to freshwater sites. *Amphora turgida* (PCC r=0.65) was found to be strongly associated with brackish water sites as were *Navicula tripunctata* (PCC r=0.65) and *Achnanthidium reidensis* (PCC r=0.63). Species related to hypersaline sites included *Hantzschia baltica* (PCC r=0.68), *Navicula salinicola* (PCC r=0.60) and *Amphora coffeaeformis* (PCC r=0.82).

Discussion

The study showed that 9 sites were freshwater (<3 ppt), 17 brackish (3–10 ppt), 12 saline (10–50 ppt) and 13 hypersaline (>50 ppt). The majority of wetlands were considered to be saline, following previously documented research on waterbodies in this region (Geddes *et al.* 1981; Williams 1983; Schofield *et al.* 1988; Kay *et al.* 2001; Cale *et al.* 2004). However, salinity at the sites varied greatly as a result of the season in which one-off sampling took place, as well as the intermittent nature of many of the lakes and streams situated in the wheatbelt. The warmer temperatures experienced over summer and autumn cause a rise in salinity as more salt is concentrated, a process that is exacerbated by the shallow nature of inland systems (Williams 1983; Chhabra 1996). With the onset of winter rains the
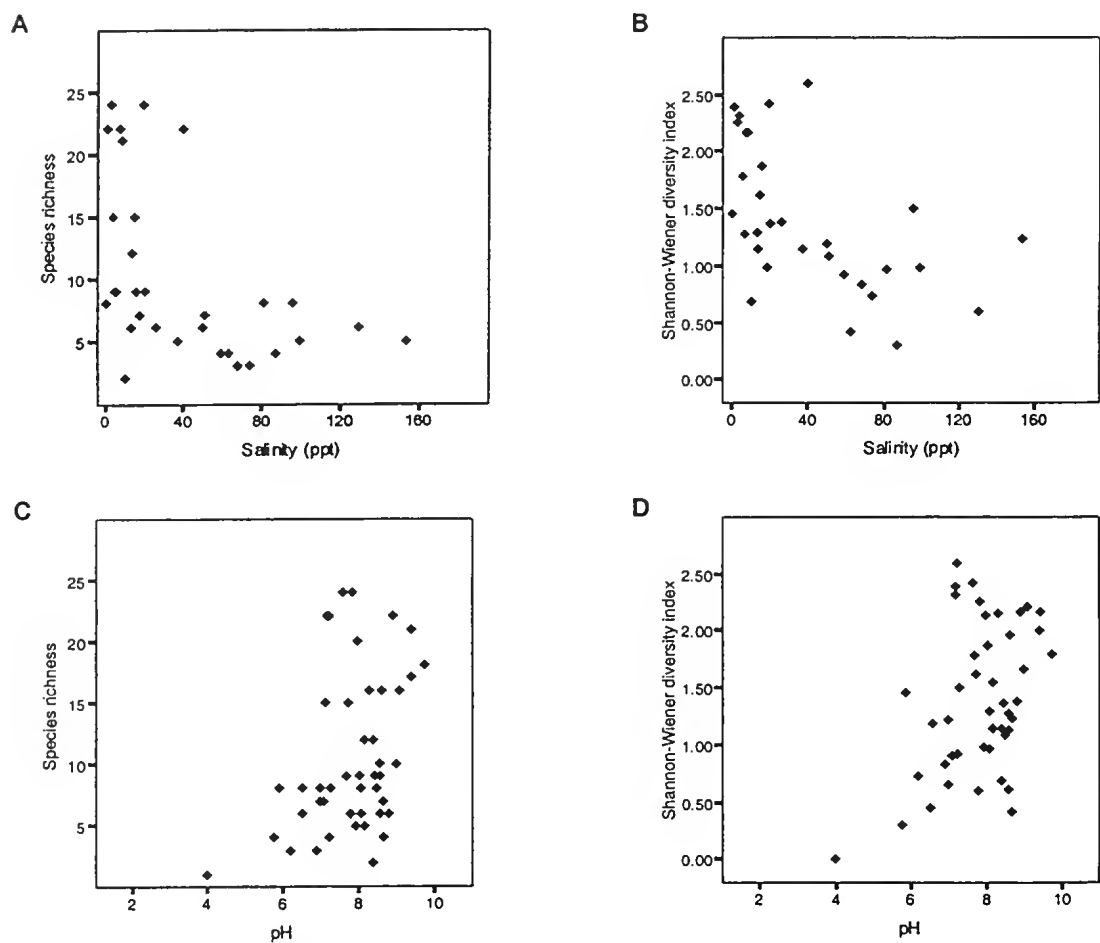
Figure 2. Scatterplots of diatom species richness and Shannon-Wiener diversity index for wheatbelt sites in relation to salinity (A & B), and pH (C & D).
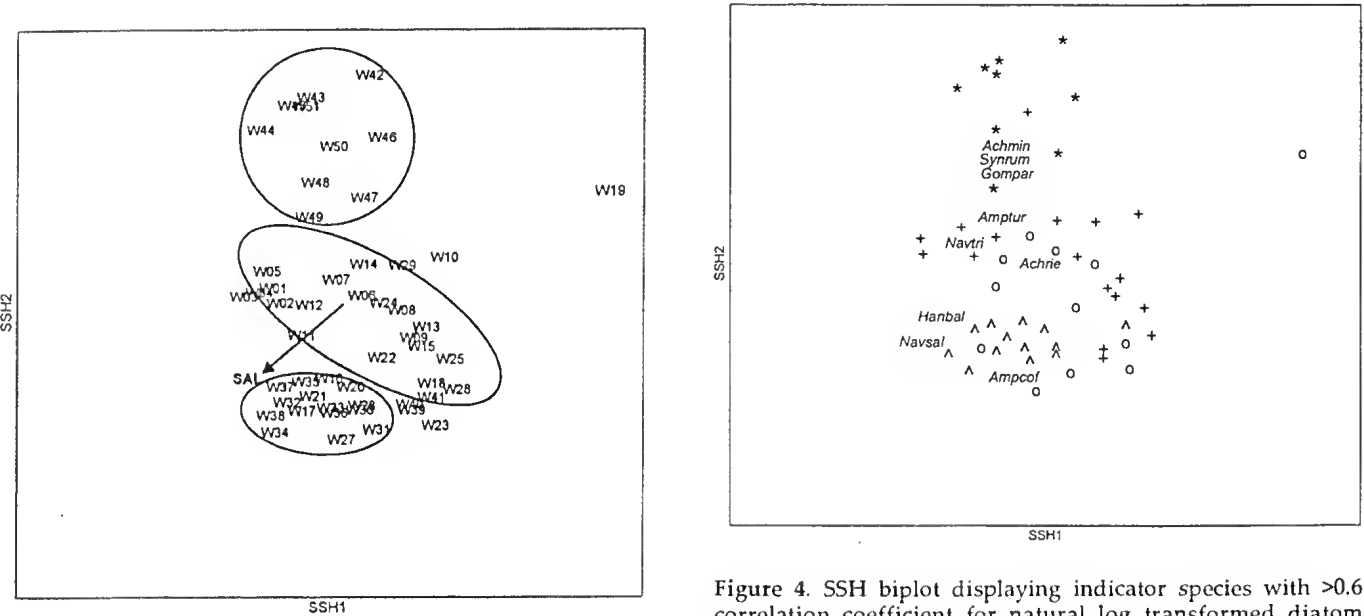
Figure 3. SSH biplot for salinity using >10 % frequency of natural log diatom species from 51 wheatbelt sites. The salinity vector (SAL) has been superimposed, showing the gradient from low to high salinity concentration. Upper circle represents freshwater (3 ppt) sites, middle circle indicates brackish (3-10 ppt) and saline (10-50 ppt) sites; lower circle denotes hypersaline (> 50 ppt) sites.

Figure 4. SSH biplot displaying indicator species with >0.6 correlation coefficient for natural log transformed diatom abundances and >10 % frequency of species, where (*) are freshwater sites, (+) are brackish sites, (o) are saline sites and (^) are hypersaline sites. Achmin – *Achnanthidium minutissimum*, Synrum – *Synedra rumpens* var. *scotica*, Gompar – *Gomphonema parvulum*, Amptur – *Amphora turgida*, Navtri – *Navicula tripunctata*, Achrie – *Achnanthidium reidensis*, Hanbal – *Hantzschia baltica*, Navsal – *Navicula salinicola*, Ampcof – *Amphora coffeaeformis*.

majority of wetlands are subjected to an influx of freshwater, generating flushing and lowering salinity levels. This was the case for sites such as Yenyening Lake (W27), which was sampled immediately following heavy rainfall, recording a salinity of 17.70 ppt – a marked decrease from its usual hypersaline condition (Weaving 1999).

The salinity of waterbodies is also affected by surrounding land use practices. Drainage channels from surrounding farmland generate saline runoff that increases stream salinities and enters larger river systems. This situation commonly occurs at sites along the Avon River such as Katrine Bridge (W11) and Glen Avon Pool (W12), which experience a rise in salinity as a result of hypersaline inflows from surrounding tributaries (Schofield et al. 1988; Avon River System Management Committee 1993).

Diatom assemblages from the wheatbelt lakes and streams varied greatly, with the highest number of species from the genera *Nitzschia*, *Amphora* and *Navicula*. An inverse relationship was shown between species richness/Shannon-Wiener diversity index and salinity. This supports findings from studies on groups of biota including riparian vegetation (Halse et al. 1993; Lymbery et al. 2003), invertebrates (Geddes et al. 1981; Halse et al. 2003; Cale et al. 2004) and waterbirds (Cale et al. 2004) conducted on wetlands in this area.

The ordination indicated that salinity was a key factor influencing diatom community structure, with a clear distinction between freshwater and hypersaline sites. The substantial difference in the species composition between these two categories is to be expected due to the large variation in salinity, which ranged from less than 0.15 ppt to almost 155 ppt over the sites. The distinction between brackish and saline sites however was less apparent, showing diatom assemblages within these water bodies have broader tolerance limits. Williams (1998) has previously stated that biota typical of freshwaters generally have a lower salinity tolerance, compared to species inhabiting saline conditions, which can withstand a wider range of concentrations.

Ardath Lake (W19) was completely isolated from all sites according to the ordination procedure. This was due to its acidic (pH<4) and saline (>25 ppt) nature resulting in a single species of diatom (*Nitzschia pusilla)* occurring at this site. This species has been shown to have a preference for acidic environments as well as having a high salinity tolerance (Sims 1996). Naturally acidic/ saline wetlands are common in the Bruce Rock area where Ardath Lake is located and are caused by local hydrogeochemical characteristics (Mann 1983). However, the problem of acidification due to fertiliser use and the installation of deep drains that promote acidic runoff is becoming cause for concern (Archer 2001; Halse et al. 2003).

The ordination also generated indicator species that were highly correlated with site groupings. Diatoms correlated with freshwater sites included *Achnanthidium minutissimum*, *Synedra rumpens* var. *scotica* and *Gomphonema parvulum*. These diatoms have been previously documented from freshwater lakes and streams by Fontes et al. (1995), Ehrlich & Ortal (1979) and John (1984). Taxa associated with brackish waters included *Achnanthidium reidensis, Amphora turgida* and *Navicula tripunctata*, which have been found to tolerate high salinity conditions by Foged (1978). The latter two species have also been described from brackish/saline environments by Patrick & Reimer (1966; 1975). Hypersaline waterbodies were dominated by *Hantzschia baltica*, *Navicula salinicola* and *Amphora coffeaeformis*. In particular *Amphora coffeaeformis* has been recognised as a highly salt tolerant diatom throughout the world as well as in the eastern states of Australia (Gell & Gasse 1990; Gell et al. 2002) and Western Australia (John 1998).

The distribution pattern of diatoms is influenced by many factors including physical conditions as well as water chemistry. However, this study concentrated on salinity, analysing the distribution pattern of diatoms through the investigation of species tolerance ranges. The results obtained from this study reinforce the advantages of using diatoms as indicators to monitor salinisation of

Table 4

Species richness of diatoms from the 51 coded wheatbelt sites, where (*) are freshwater sites, (+) are brackish sites, (o) are saline sites and (^) are hypersaline sites.

	Site	Species richness		Site	Species richness		Site	Species richness
+	W01	17	^	W18	8	^	W35	8
+	W02	21	o	W19	1	^	W36	5
+	W03	16	^	W20	4	^	W37	5
+	W04	18	^	W21	3	^	W38	6
+	W05	22	o	W22	9	+	W39	2
o	W06	22	o	W23	6	+	W40	9
o	W07	24	+	W24	6	o	W41	3
o	W08	12	+	W25	12	*	W42	8
+	W09	8	+	W26	9	*	W43	7
+	W10	10	o	W27	7	*	W44	8
o	W11	9	^	W28	4	*	W45	14
o	W12	15	+	W29	16	*	W46	16
+	W13	16	^	W30	7	*	W47	8
+	W14	15	o	W31	6	*	W48	20
+	W15	10	o	W32	5	*	W49	7
^	W16	3	^	W33	5	+	W50	24
^	W17	6	^	W34	4	*	W51	22

waterbodies in the wheatbelt area. With an increased database of diatom distribution in wheatbelt lakes and streams of Western Australia a comprehensive predictive model could potentially be derived for salinisation. This model is currently being developed for incorporation into future management plans to assess the effectiveness of remediation measures undertaken for secondary salinity in WA.

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Appendix 1

List of diatom taxa identified from the 51 wheatbelt lakes and streams, indicating the number of sites in which they occurred, in order from the most common to least common.

Taxa Name	Number of occurrences	Taxa Name	Number of occurrences
Amphora coffeaeformis (Ag.) Kütz.	40	*Nitzschia fasciculata* Grun.	5
Cocconeis placentula (Ehr.) Hust.	21	*Surirella ovalis* Bréb.	5
Navicula tripunctata (O.F. Müller) Bory.	20	*Amphora acutiuscula* Kütz.	4
Hantzschia baltica Simon.	19	*Brachysira aponina* Kütz.	4
Navicula salinicola Hust.	19	*Camphylodiscus clypeus* Ehr. var. *bicostata* (W.Smith) Hust.	4
Entomoneis tenuistriata John	16	*Cocconeis placentula* var. *euglypta* (Ehr.) Cl.	4
Navicula salinarum Grun.	15	*Cyclotella striata* (Kütz.) Grun.	4
Nitzschia acicularis (Kütz.) W.Smith	15	*Entomoneis alata* Kütz.	4
Tryblionella hungarica Grun.	15	*Mastogloia halophila* John	4
Achnanthidium reidensis Foged	14	*Nitzschia pusilla* Grun.	4
Cymbella pusilla Grun.	14	*Pleurosigma elongatum* W.Smith	4
Thalassiosira weissflogii (Grun.) Fryxell & Hasle	14	*Tabularia tabulata* (Ag.) Snoeijs	4
Amphora veneta Kütz.	13	*Amphora montana* Kütz.	3
Bacillaria paxillifer (O.F. Müller) Hendey	12	*Eunotia curvata* (Kütz.) Lagerstedt.	3
Cyclotella atomus Hust.	12	*Navicula subrhynocephala* Hust.	3
Pleurosigma salinarum Grun.	11	*Nitzschia amphibia* Grun.	3
Amphora turgida Hust.	10	*Nitzschia gracilis* Hantzsch	3
Cyclotella meneghiniana Kütz.	10	*Nitzschia palea* (Kütz.) W.Smith	3
Mastogloia braunii Grun.	10	*Pinnularia lata* (Bréb.) W.Smith	3
Synedra ulna (Nitzsch) Ehr.	10	*Rhaphoneis surirella* (Ehr.) Grun. *ex* V.H.	3
Amphora holsatica Hust.	9	*Stauroneis pachycephala* Cl.	3
Navicula cryptocephala (Kütz.)	9	*Achnanthidium lanceolatum* Bréb. *ex* Kütz.	2
Navicula elegans W.Smith	9	*Amphora mexicana* A. Schmidt.	2
Rhopalodia gibberula (Ehr.) O.F.Müller	9	*Cymbella minuta* Hilse *ex* Rabh.	2
Stauroneis spicula Hickie	9	*Eunotia pectinalis* (O.F. Müller) Rabh.	2
Achnanthidium minutissimum (Kütz.) Czarn.	8	*Navicula auriculata* Hust.	2
Gyrosigma kutzingii (Grun.) Cl.	8	*Fallacia pygmeae* (Kütz.) Mann	2
Achnanthidium oblongella Oestrup	7	*Nitzschia linearis* W.Smith	2
Amphora ventricosa Greg.	7	*Rhopalodia musculus* (Kütz.) O.Müller	2
Diploneis subovalis Cl.	7	*Amphora australiensis* John	1
Nitzschia hummii Hust.	7	*Mastogloia pumila* (Grun.) Cl.	1
Gomphonema parvulum (Kütz.) Kütz.	6	*Mastogloia smithii* Thwaites.	1
Nitzschia sigma (Kütz.) W.Smith	6	*Navicula ramosissima* (Ag.) Cl.	1
Rhopalodia gibberula var. *globosa* Hust.	6	*Nitzschia obtusa* var. *scalpelliformis* Grun.	1
Ctenophora pulchella (Ralfs *ex* Kütz.) Williams & Round	6	*Stauroneis dubitabilis* Hust.	1
Synedra rumpens Kütz. var. *scotica* Grun.	6	*Synedra acus* Kütz.	1

Pollen in the surface sediments of wetlands in the Becher Point area, southwestern Australia: a baseline for use in interpreting Holocene sequences

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Abstract

Pollen was collected from the surface sediments of 16 wetland basins situated on a beachridge plain in the Becher Point area, southwestern Australia. Sampling was undertaken to determine the ratio of wetland/upland plant species contributing to the surface pollen in each wetland, to determine the contributions of local and regional pollen, and to develop indicator pollen assemblages as a baseline to interpret fossil Holocene sequences. The main wetland plant assemblages colonising the wetlands include sedges – *Baumea articulata* (R. Br.) S. T. Blake;. *Typha* L. spp.; mixed *Baumea articulata* and *Typha* spp.; *Isolepis nodosa* (Rottb.) R. Br.; *Baumea juncea* (R. Br.) Palla; *Lepidosperma gladiatum* Labill.; rushes – *Juncus krausii* Hochst.; grasses – *Sporobolus virginicus* (L.) Kunth.; shrubs – *Melaleuca viminea* Lindley; *Melaleuca teretifolia* Endl.; grass trees – *Xanthorrhoea preissii* Endl.; trees and shrubs – *Melaleuca rhaphiophylla* Schauer, *Melaleuca cuticularis* Labill. The pollen assemblages recovered from the surface sediments were separated into six categories as related to extant vegetation: that generated *in situ* from wetland basin vegetation; that derived from *in situ* wetland margin vegetation; that derived allochthonously from wetland vegetation; that from ridge vegetation (inhabiting the beachridges) and transported to the wetland basin; that from distal vegetation in the region; and uncategorised pollen. Of the plants extant in modern wetland centres and their margins, the following key species were commonly detected as pollen grains in the surface sediment: *Centella asiatica* (L.) Urban, *Baumea articulata*, *Baumea juncea*, *Isolepis nodosa*, *Lepidosperma gladiatum*, *Melaleuca cuticularis*, *Melaleuca viminea*, *Melaleuca rhaphiophylla*, *Melaleuca teretifolia*, *Sporobolus virginicus*, *Typha domingensis* Pers./*T. orientalis* C. Presl, and *Xanthorrhoea preissii*. In most wetlands, the majority of the surface pollen in the wetlands was derived from the local wetland and upland ridge vegetation (*i.e.*, that inhabiting the beachridges) of the cuspate foreland. Generally, *in situ* wetland pollen constituted a moderate proportion of the total pollen. Wetland margin pollen was abundant in only half the wetlands. Pollen from ridges was sub-dominant to pollen from allochthonous wetland species in about half the wetlands, and dominant in the remainder. The contribution of distal pollen varied from low in most wetlands to relatively high numbers and significant in others.

The potential dispersal mechanisms for pollen in this area are insects, avifauna, local processes of *in situ* generation, and easterly and westerly winds, and transport agents include wind, rain, sheet wash, and water transport. The differential effect of wind in transporting pollen was explored using local wetland species of *Melaleuca* as a signature, and the occurrence of upland species, such as Casuarinaceae spp., *Olearia axillaris* (DC.) F. Muell. ex Benth., and *Eucalyptus marginata* Donn ex Smith pollen. The patterns show that delivery of pollen to the wetland basins is heterogeneous.

Keywords: palynology, Holocene, wetlands, Becher Point, southwestern Australia

Introduction

The wetlands in the Becher Suite, in the Becher Point area, occur on a Holocene beachridge plain in southwestern Australia (Fig. 1), and comprise numerous small-scale inter-dune basins with a range of vegetation associations that vary from basin to basin (C A Semeniuk

2006). While there is topographic variation in the height of local beachridges, (+ 2–3 m), the basins of the Becher Suite essentially reside in an area with relatively homogeneous geomorphology, stratigraphy, hydrochemistry, and climate *i.e.*, the Becher cuspate foreland (Searle *et al.* 1988).

Palynological studies in Western Australia, using only one or two cores in large water-filled basins, such as Lake Gnangara, Lake Thompson, and North Lake, with
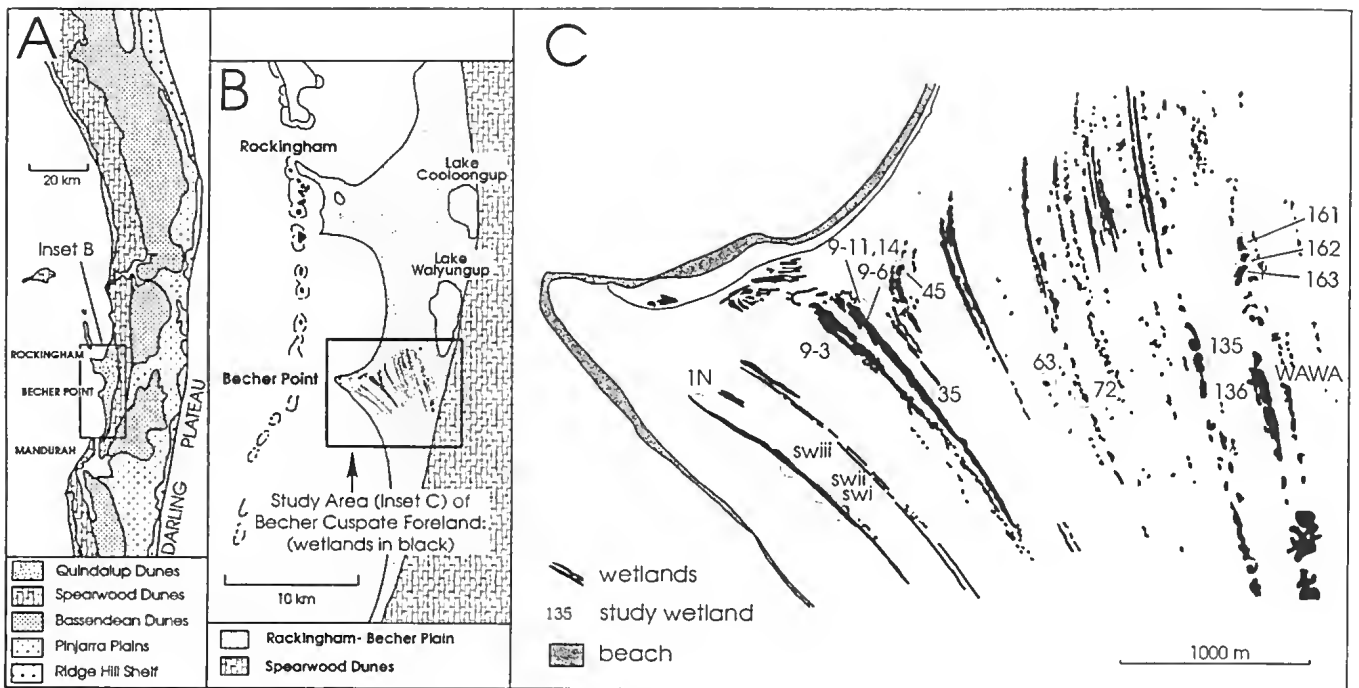
Figure 1. A. Location of Study Area in southwestern Australia. B. The Becher Point area and the Cuspate Foreland. C. Wetlands of the Becher Point area; basins selected for study are circled and annotated.

variable internal hydrodynamic processes, varied peripheral vegetation traps, and likely complex intrabasinal sediment transport, may provide a biased pollen record and impact on the interpretation of local vegetation and climate history. To date, in Western Australia, there have been no published studies directed towards determining the heterogeneity of the pollen record in the large isolated wetland basins, even though studies elsewhere have indicated the complexities inherent in the accumulation of pollen (Dodson 1983; D'Costa & Kershaw 1997; Luly 1997).

Although the area of wetland on the Becher cuspate foreland is equivalent to the large lakes of the Swan Coastal Plain (Fig. 1), the multiplicity of small basinal sinks within it provide, not one, but a series of replicate pollen capture zones, as well as a measure of how consistently pollen reflects the subregional and regional vegetation, and hence climate setting. Inter-basin variation in wetland plant assemblages provides a means to replicate the measure of how effectively *in situ* pollen production is reflected by the pollen record. Thus, the small-scale and numerous wetland basins of the Becher Suite, provide a rare opportunity to examine the relative contributions of autochthonous, and proximal and distal allochthonous pollen to contemporary pollen assemblages.

The specific objectives of this study were to investigate the relationship between present day pollen accumulation and present day vegetation in the wetlands and surrounds of the Becher cuspate foreland; firstly, to determine the ratio of wetland/upland species contributing to the surface pollen assemblages in each wetland; secondly, to determine the various contributions to the wetland basin of local and regional pollen; and, thirdly, to use the surface pollen assemblages as a baseline to interpret fossil sequences (the subject of a later

paper). For this study, the pollen of the surface sediments was investigated for 16 wetland basins (Fig. 1) for which there were data on the vegetation associations. A wide variety of wetland vegetation types were selected in order to encompass as many pollen assemblages as possible, and to determine whether the processes of pollen transport and preservation varied over the cuspate foreland.

Materials and methods

The wetlands selected for palynological study of their surface sediments were 161, 162, 163, WAWA, 135, 136, 72, 45, 35, 9-3, 9-6, 9-14, swi,swii, swiii, 1N (Fig. 1). The upper 1 cm of sediment from the surface, and in wetlands with a thick cover of leaf litter, samples from the surface litter were collected in the centre of each of these wetlands. Calcilutite in these wetlands has accumulated at a rate of 0.1–0.4 mm/yr (C A Semeniuk 2006), and therefore if sedimentation has continued into the present, the sampling interval represents at least 25–100 years of accumulation.

To provide an appreciation of the variability of vegetation assemblages in these wetlands, a programme of vegetation mapping, classification and quantitative analyses was undertaken during 1991–2001, with the quantitative studies occurring in three intervals for intra-decadal comparative purposes over the 10 years of study (C A Semeniuk 2006). The quantitative intra-decadal studies provided information on how stable the composition of the vegetation assemblages were against a background of declining water levels (C A Semeniuk 2006), and whether the pollen record in the surface sediments would reflect these short term compositional changes in vegetation. Wetland vegetation was classified into assemblages based on species composition and

structure. The distribution of these assemblages was mapped within each wetland basin. Transects were established across the basins to document gradients in vegetation composition. Assemblage composition was quantified in replicate quadrats, and classified using numerical classification techniques. The results of this programme are presented in more detail in C A Semeniuk (2006), but relevant aspects as they relate to describing vegetation associations for the composition of surface pollen in wetlands are presented briefly later in this paper.

Reference pollen was collected from living plant species colonising the wetlands and ridges in the region, as well as from herbarium sheets held by the W A Herbarium for species cited in the literature. Pollen samples were acetolysed following the standard technique of Erdtman (1960), as outlined by Phipps & Playford (1984).

Sediment samples were processed to extract the organic material following the general procedures of Phipps & Playford (1984). To assess the pollen content in each sample, a 0.2 ml suspension of pollen from an exotic (alien) species (from the Betulaceae) was added to each sample prior to processing (*circa* 2,700 ± 400 grains of Betulacid pollen per cm³ of sediment).

In each sample, the multiplied by the ratio of added Betulacid pollen to Betulacid pollen counted. Pollen identification wasBetulacid pollen was counted along with a total of two hundred pollen grains from the sediment. Total pollen in a given standard volume of sediment (*e.g.*, a cubic centimetre) was calculated from the counted pollen referred to prepared modern pollen standards, referenced to publications, or assigned to an "uncategorised" group.

A mathematical problem potentially occurs for pollen taxa with a count of zero in the volume of sample prepared. In multiplying the actual counted numbers of pollen of native plants by the ratio of Betulacid pollen added in a cubic centimetre of sediment to the number of Betulacid pollen recorded in order to transform the numbers of pollen of native species into abundances per cubic centimetre, zero still remains zero in contrast to all other taxa which increase proportionately. In fact, pollen recorded as zero in a low volume of sediment may have been detected in larger volumes of sediment, albeit in low numbers. Nonetheless, those pollen from native species which scored zero from a count of 200 pollen grains indicate either relative very low abundance in a cubic centimetre of sediment, or indeed absence.

Regional setting, local geomorphology, age structure and description of wetlands selected for study

The Rockingham-Becher Plain, as part of the Quindalup Dunes (McArthur & Bettenay 1960; Semeniuk *et al.* 1989), located in the larger physiographic unit of the Swan Coastal Plain, is a twin accretionary cuspate foreland system comprising a beachridge plain (Semeniuk & Searle 1986), extending from Cockburn Sound in the north to the Peel-Harvey Estuary exchange channel in the south (Fig. 1). The Spearwood Dune Ridge forms the eastern border of the beachridge plain. The basin wetlands of the Becher Suite are located in the inter-dune depressions or swales of the beachridge plain on the southern cusp of the twin

cuspate foreland whose apex is Becher Point. As described by Searle *et al.* (1988) and C A Semeniuk (2006), the coastal plain here consists of a series of parallel beachridges of height 2–3 m above AHD, with local ridges 3–8 m above AHD, *circa* 6000 years in age at its eastern part and 500 years in age to contemporary at its shore. The wetlands range in age from *circa* 4500 years in eastern parts of the beachridge plain to *circa* 680 years in the western parts. At the local scale, the individual wetland basins occur discontinuously along the axis of a beachridge swale and are generally flanked to east and west by beachridges and to north and south by sand structures that partition the longitudinal inter-dune depressions.

The wetland basins of the Becher Suite are filled with calcilutaceous muddy sand, calcilutite, quartz-calcareous sand, and peat (C A Semeniuk 2006). Sedimentary fill generally is < 1 m thick. The wetland vegetation has been described by C A Semeniuk (2006). This vegetation can be categorised, in general terms, into assemblages relative to the centre and to the margins of the wetlands: an inner, "core-of-wetland" assemblage, and an outer, peripheral assemblage. The plant assemblages identified by C A Semeniuk (2006) are:

1. *Centella asiatica (L.)* Urban herb assemblage
2. *Baumea articulata* (R. Br.) S. T. Blake sedge assemblage
3. *Typha* L. sp. sedge assemblage
4. mixed *B. articulata* and *Typha* sp. sedge assemblage
5. *Juncus kraussii* Hochst rush assemblage
6. *Melaleuca teretifolia* Endl. shrub assemblage
7. *Melaleuca rhaphiophylla* Schauer forest or shrub assemblage, with understorey of *C. asiatica* (L.) Urban
8. *Melaleuca cuticularis* Labill. forest assemblage
9. wetland margin *Melaleuca viminea* Lindley heath
10. wetland margin of *Xanthorrhoea preissii* Endl. with understorey of *Isolepis nodosa* (Rottb.) R. Br. sedge assemblage and *Sporobolus virginicus* (L.) Kunth. grass assemblage
11. wetland margin of *I. nodosa* sedge assemblage
12. wetland margin of *S. virginicus* grass assemblage
13. wetland margin of *Baumea juncea* (R. Br.) Palla sedge assemblage
14. wetland margin of *Lepidosperma gladiatum* Labill. sedge assemblage

The key plants within each of the selected wetlands are described in Table 1.

Species contributing to the pollen record

The species pool

A variety of plant species contribute pollen to the wetlands of the Becher Point area. These occur in the wetlands and on the ridges on the Becher Cuspate Foreland, and from terrain further east (Tables 2–4). For a more comprehensive description of the vegetation on the cuspate foreland refer to C A Semeniuk (2006).

Table 1

Description of wetlands in this study in terms of location relative to age structure, wetland type, sedimentary fill, and vegetation

Wetland	Geographic and implied age setting	Local geomorphic setting	Wetland type	Sediment fill	Structurally and numerically dominant species
161	older eastern part of suite	relatively high beachridges border east and west margins	sumpland	calcilutite, and basal calcilutaceous muddy sand	*Baumea articulata*
162	older eastern part of suite	relatively high beachridges border east and west margins	sumpland	calcilutite, and basal calcilutaceous muddy sand	*Melaleuca teretifolia*
163	older eastern part of suite	relatively high beachridges border east and west margins	sumpland	calcilutite, and basal calcilutaceous muddy sand	*Juncus kraussii*
WAWA	older eastern part of suite	relatively high beachridge borders east margin; low beachridge on west margin	sumpland	peat, calcilutite, and basal calcilutaceous muddy sand	*B. articulata, Typha orientalis*
135	middle age, central part of suite	relatively high beachridge borders east margin; low beachridge on west margin	sumpland	calcilutite, and basal calcilutaceous muddy sand	*M. rhaphiophylla, Centella asiatica*
136	middle age, central part of suite	relatively high beachridge borders east margin; low beachridge on west margin	sumpland	calcilutite, and basal calcilutaceous muddy sand	*M. rhaphiophylla, C. asiatica*
72	middle age, central part of suite	relatively high beachridges border east and west margins	dampland	calcilutite, and basal calcilutaceous muddy sand	*B. juncea, C. asiatica*
45	middle age, central part of suite	low beachridges border east and west margins	sumpland	calcilutite, and basal calcilutaceous muddy sand	*M. rhaphiophylla, C. asiatica*
35	middle age, central part of suite	low beachridges border east and west margins	sumpland	calcilutite, and basal calcilutaceous muddy sand	*M. rhaphiophylla, J. kraussii, C. asiatica*
9-3	younger western part of suite	relatively high beachridge borders west margin; low beachridge on east margin	sumpland	calcilutite, and basal calcilutaceous muddy sand	*B. juncea*
9-6	younger western part of suite	low beachridges border east and west margins	sumpland	calcilutite, and basal calcilutaceous muddy sand	*B. juncea, C. asiatica*
9-14	younger western part of suite	low beachridges border east and west margins	sumpland	calcilutite, and basal calcilutaceous muddy sand	*J. kraussii*
swi	younger western part of suite	low beachridges border east and west margins	dampland	calcilutite, and basal calcilutaceous muddy sand	*Lepidosperma gladiatum*
swii	younger western part of suite	low beachridges border east and west margins	dampland	calcilutite, and basal calcilutaceous muddy sand	*L. gladiatum*
swiii	younger western part of suite	low beachridges border east and west margins	sumpland	calcilutite, and basal calcilutaceous muddy sand	*Schoenoplectus validus* (M. Vahl) A. Love & D. Love
1-N	younger western part of suite	low beach ridges border east and west margins	dampland	calcilutite, and basal calcilutaceous muddy sand	*B. juncea*

Table 2

Main plant species within wetlands in the Becher Point area

Perennial species		Annual species	
Family	Species	Family	Species
Apiaceae	*Centella asiatica* (L.)	Compositae	**Sonchus asper* Hill
Chenopodiaceae	*Halosarcia halocnemoides* (Nees) Paul G. Wilson	Papilionaceae	**Trifolium* L. spp.
Cyperaceae	*Baumea articulata*	Crassulaceae	**Crassula* L. sp.
	B. juncea	Brassicaceae	**Brassica tournefortii* Gouan
	*Cyperus sp.	Iridaceae	**Romulea* sp.
	Isolepis nodosa		
	Isolepis cernua (M. Vahl) Roemer & Schultes		
	Lepidosperma gladiatum		
	Schoenoplectus validus		
	Typha domingensis		
	*T. orientalis		
Geraniaceae	**Pelargonium capitatum* (L.) L'Her.		
Juncaceae	*Juncus kraussii*		
Juncaginaceae	*Triglochin striata* Ruiz Lopez & Pavon or		
	Triglochin mucronata R. Br.		
Lobeliaceae	*Lobelia alata* Labill.		
Myrtaceae	*Melaleuca cuticularis*		
	M. viminea		
	M. rhaphiophylla		
	M. teretifolia		
Poaceae	*Sporobolus virginicus*		
Primulaceae	*Samolus repens* (Forster & G. Forster) Pers.		
Verbenaceae	**Phyla nodiflora* (L.) E. Green		
Xanthorrhoeaceae	*Xanthorrhoea preissii*		

* denotes alien species

Table 3

Main plant species on beachridge/dunes of the Becher Cuspate Foreland

Family	Perennial species
Chenopodiaceae	*Rhagodia baccata* (Labill.) Moq.
Compositae	*Olearia axillaris* (DC) F. Muell. et Benth.
Cyperaceae	*Lepidosperma squamatum* Labill.
	Schoenus grandiflorus (Nees) F. Muell.
Dasypogonaceae	*Acanthocarpus preissii* Lehm.
	Lomandra maritima Choo
Epacridaceae	*Leucopogon parviflorus* (Andrews) Lindley
Euphorbiaceae	*Adriana quadripartita* (Labill.) Gaudich.
	Phyllanthus calycinus Labill.
Geraniaceae	**Pelargonium capitatum*
Haemodoraceae	*Conostylis aculeata* R. Br.
Mimoseae	*Acacia cyclops* Cunn. ex Don
	Acacia lasiocarpa Benth.
	Acacia pulchella R. Br.
	Acacia rostellifera Benth.
	Acacia saligna (Labill.) H. L. Wendl.
Myrtaceae	*Melaleuca systena* (formerly
	M. acerosa Schauer)
Poaceae	*Austrostipa flavescens* (Labill.)
	S W L Jacob, J Everett
Proteaceae	*Hakea prostrata* R. Br.
	Jacksonia furcellata (Bonpl.) DC.
Rhamnaceae	*Spyridium globulosum* (Labill.) Benth.
Santalaceae	*Exocarpos sparteus* R. Br.

* denotes alien species

Table 4

Key plant taxa as pollen sources from areas east of the wetlands on Becher Point

Family	Perennial species
Casuarinaceae	*Allocasuarina fraseriana* (Miq.) L. Johnson
	Casuarina humilis (Otto & Dietr.) L. Johnson
Myrtaceae	*Eucalyptus gomphocephala* DC.
	Eucalyptus marginata
	Hypocalymma robustum (Endl.) Lindley
Proteaceae	*Banksia attenuata* R. Br.
	Banksia menziesii R. Br.
	Banksia grandis Willd.

Preservation of pollen and its differential destruction in the sediment

The pollen derived from wetland plants and species on the adjacent ridges has variable natural preservation and variable resistance to the laboratory process of acetolysis. In the former context, pollen from the following families are well preserved and common: Casuarinaceae, Compositae and Poaceae. In the latter context, pollen grains which are often destroyed or badly damaged by acetolysis (Nilsson and Praglowski 1992), include those of Juncaceae. Therefore, the absence of this pollen from surface and core samples cannot be interpreted as indicating absence of species of Juncaceae in the wetland basin or surrounds. These remarks particularly pertain to wetland basins in which *Juncus kraussii* occurs or is dominant. Some Myrtaceae and Cyperaceae pollen grains also show susceptibility to

degradation, both as a result of the processing method and of oxidation.

Of the plants extant in modern wetland centres and their margins, the following key species were commonly detected as pollen grains in the sediments:

Centella asiatica

Baumea articulata

Baumea juncea

Isolepis nodosa

Lepidosperma gladiatum

Melaleuca cuticularis

Melaleuca rhaphiophylla

Melaleuca teretifolia

Melaleuca viminea

Sporobolus virginicus

Typha domingensis (or *T. orientalis*)

Xanthorrhoea preissii

Pollen transport and deposition

Potential dispersal processes and transporting agents for pollen include easterly and westerly winds, insects, avifauna, rain, local processes of *in situ* generation, sheet wash, and water transport. These processes are summarised in Figure 2.

In Western Australia there is scant information about pollen dispersal mechanisms for many plants, and this is particularly the case for Cyperaceae, species of which dominate the Becher wetlands. Pollen from Xanthorrhoeaceae and Myrtaceae, in particular *Melaleuca*, is dispersed by both insects and avifauna (Brown *et al.* 1997), and Casuarinaceae, a prolific pollen producer disperses its pollen by wind (Backhouse 1993). In lieu of data about specific dispersal mechanisms for pollen from wetland plants, some general observations about the effects on pollen dispersal within the setting of the Becher Suite wetlands are made. These relate to wind patterns, vegetation on the Spearwood Ridge and the Cooloongup and Walyungup wetlands to the east, local topography, and type of vegetation structure at the wetland margin, complemented by the actual occurrence of pollen species on the wetland surface and in cores.

In the Becher Point region, modern dispersal of pollen by wind would be related to the prevailing northeasterly and southwesterly winds typical of spring, and the west to south westerly seabreezes and the easterly quadrant landbreezes, both dominant in summer (Searle & Semeniuk 1985). The pattern of dispersal along these trajectories would result largely in a redistribution of pollen within the cuspate foreland, but pollen could also be transported from vegetation on the higher (Holocene) ridges in the Cooloongup Lake area and from the bordering Spearwood Dune Ridge (Fig. 1). Plant communities on the Holocene sand ridges at Lake Cooloongup comprise similar species to the ridges in the Becher Point region, with the important addition of tall woodland of *Eucalyptus gomphocephala*. The vegetation on the Spearwood Dune Ridge is *E. marginata/Banksia* spp. low woodland. On the Becher cuspate foreland,

pollen derived from local ridges and sub-regionally may be deposited in the wetlands directly by rain or by sheet wash from the ridges to the wetland margins. As the wetlands are located in swales, it is unlikely that pollen deposited onto the litter or sediment of the vegetated wetland basins would be remobilised.

The topography of the Becher cuspate foreland is composed of relatively low parallel ridges, but locally interspersed in this landscape are higher than average ridges which are approximately 3–8 m above the adjoining swale. These higher ridges are likely to have some impact on the amount and type of pollen deposited in any wetland on the lee side of the ridge. By forming a partial obstruction to easterly and northeasterly wind flows, the ridge can cause wind to rise from the relatively flatter and lower surface of the plain, initially increasing its velocity at the ridge crest and then decreasing velocity over the adjacent wetland. Pollen, carried by the wind from regional vegetation east of the Becher Point, as well as from vegetation colonising ridge crests, is likely to be deposited in the adjoining wetland bordered by a high ridge at a greater frequency than in wetlands between lower ridges.

In wetlands situated between the lower beachridges, deposition of allochthonous pollen into the centre of the basin, where the cores were obtained, may be hampered by the type of vegetation structure at the wetland margin. In wetlands 35 and 45, for example, this vegetation is composed of *Melaleuca* trees which effectively buffer the central part of the wetland. In other wetlands, *e.g.*, wetland 162, an effective buffer is created by a lower but tightly closed canopy of *X. preissii*. Pollen raining onto a closed canopy in central parts of the wetland basin can be expected to be later remobilised to the floor of the wetland basin by rain.

Pollen generated *in situ* from wetland plants situated in swales between the adjacent ridges is subject to reduced wind frequency and velocity. The locus for wind transport is between swale and ridge rather than along the swale, unless the swale is relatively shallow, and therefore the distance that pollen is transported from one wetland basin to another along any swale is likely to be very short. The wetlands may generally be regarded as pollen sinks for both *in situ* and imported pollen from local ridges.

Surface pollen within the wetland basin may be redistributed spatially in two ways: by wind generated water movement during inundation, and by bioturbation. Redistribution under the first process is likely to be minimal because of plant buffering. Redistribution under the second process is likely to be significant at the 10 cm scale.

Results: pollen in surface sediments

The pollen record in the surface sediments in the central basin of the 16 wetlands provided a baseline of surface pollen assemblages in relation to the various types of wetland plant assemblages, species inhabiting the adjoining beachridges, and species occurring distal to the Becher Suite. In each wetland, for the analysis of surface pollen, the pollen assemblages recovered from the surface sediments were separated into six categories as related to extant vegetation:

A: AGENTS OF DISPERSAL AT THE SUBREGIONAL SCALE

RAIN

EASTERLY WINDS

WESTERLY WINDS

POLLEN DERIVING FROM RIDGES AND WETLAND BASINS (see below)

POLLEN DERIVING FROM THE SPEARWOOD DUNES
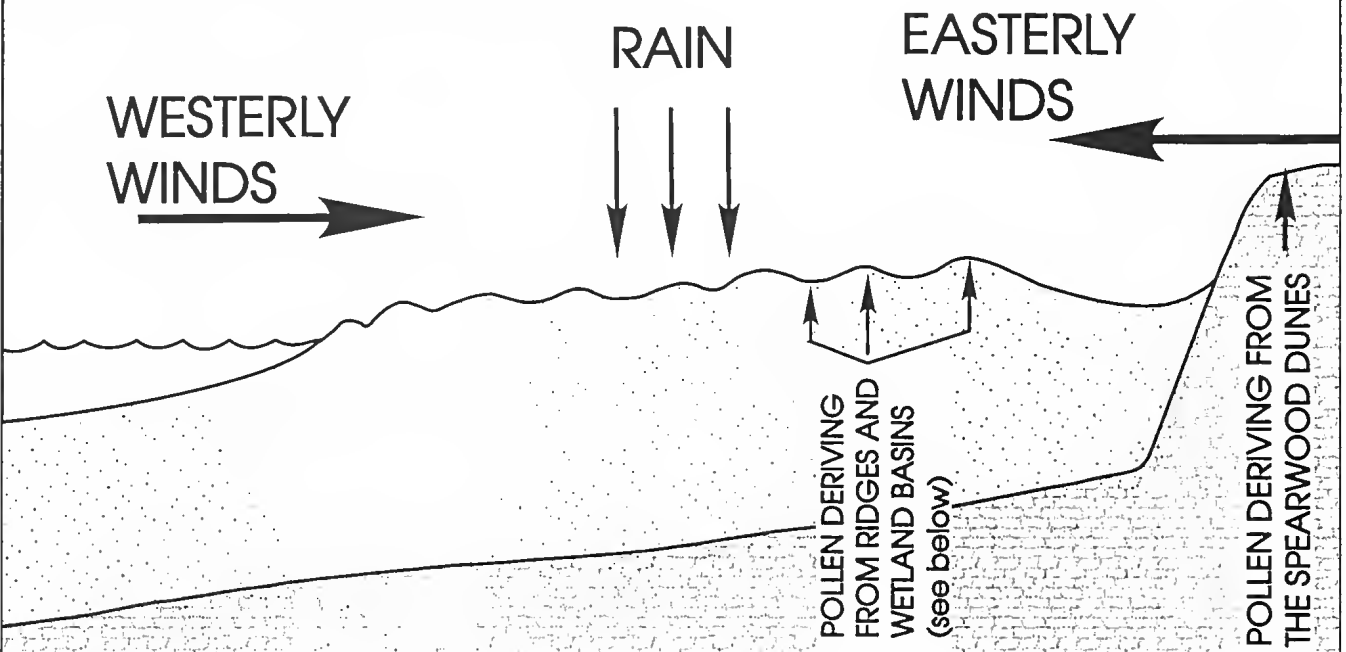
B: AGENTS OF DISPERSAL, AND ACCUMULATION OF POLLEN AT THE LOCAL SCALE

pollen from regional sources entrained in easterly winds

fall-out of pollen from easterly winds as well as entrainment by rain - sources are regional vegetation and that from local eastern ridges and wetlands

pollen from local eastern high ridge entrained by easterly winds

pollen from local western low ridge entrained by westerly winds

pollen from nearby wetlands, entrained by westerly winds

pollen from nearby wetlands, entrained by easterly winds

In situ accumulation from ridge vegetation

sheet wash transport from margins

In situ accumulation from resident wetland vegetation

sheet wash transport from margins

water transport and redistribution of pollen within wetland basin at times of inundation

Figure 2. Potential patterns of dispersal and accumulation of pollen into wetland basins with *in situ*, local, and regional sources.

1. that generated *in situ* from wetland basin vegetation;

2. that derived from *in situ* wetland margin vegetation;

3. that derived allochthonously from wetland vegetation;

4. that from ridge vegetation and transported to the wetland basin;

5. that from vegetation distal to the region;

6. uncategorised pollen.

Pollen was categorised as deriving from *in situ* wetland vegetation or *in situ* wetland margin vegetation if the pollen species corresponded to either the wetland plant species or wetland marginal species currently colonising a particular wetland basin. Pollen derived allochthonously from wetland vegetation included that from species of wetland plants currently colonising the Becher Suite wetlands elsewhere in the sub-region of the Becher cuspate foreland, but not within the basin from which the surface pollen sample was obtained. "Ridge" pollen included pollen from species colonising the beach ridges comprising the upland on the Becher cuspate foreland, and "regional" pollen was categorised as deriving from beyond the Becher cuspate foreland. The patterns arising from the variable composition of surface pollen based on the different categories are described below and illustrated in Figure 3.

Overall, the majority of the surface pollen in the wetlands has been derived locally from the wetland and upland ridge vegetation of the Becher cuspate foreland. With the exception of wetland swi, *in situ* wetland pollen constituted a moderate proportion of the total pollen found at the surface, varying from 5–44% (Fig. 4). Wetland margin pollen was abundant in only half the wetlands. Pollen from allochthonous wetland species was present in most of the wetlands, specifically pollen from

species of *Melaleuca*. "Ridge" pollen was sub-dominant to pollen from wetland species in 7 wetlands; in the remaining wetlands it was the dominant type of pollen. Overall, there is an increase from east to west in "ridge" pollen contributing to the total pollen (compare the eastern wetlands 161, 162, 163, and WAWA with centrally located wetlands 135, 136, 72, 45, 35 and 9–14, and with westermost wetlands swi, swii and swiii), probably reflecting seabreezes from westerly quadrants delivering pollen from the ridges to the adjoining wetland basin having more effect in near coastal areas. The contribution and significance of "regional" pollen varied (0–48%), from low numbers in most wetlands to relatively high numbers and significant proportions in wetlands 161 (17%), WAWA (48%), and 1N (20%). Uncategorised pollen ranged from 0–28%.

To demonstrate the relationship between extant wetland vegetation and surface pollen abundance in a particular wetland basin, the estimated cover and percent of total surface pollen for each species are summarised in Table 5.

With the exception of *J. kraussii*, pollen for most species of plants colonising the wetland basin were present in the surface sediments (Fig. 4). Pollen derived from *in situ* wetland plants was dominated by several species, *M. rhaphiophylla, S. virginicus* and *C. asiatica*. For the majority of species, the pollen numbers did not reflect the current abundance of plants in the wetlands. Pollen abundance for both species of *Baumea*, for two species of *Melaleuca* (*M. viminea* and *M. teretifolia*), and for *L. gladiatum* were consistently lower than the present vegetation cover would suggest. Pollen of *P. nodiflora* was also absent or rare even when cover abundance in a particular wetland was high, probably because of the short period of wetland colonisation by this species. Wetland plant species, *M. rhaphiophylla, S. virginicus, T.*
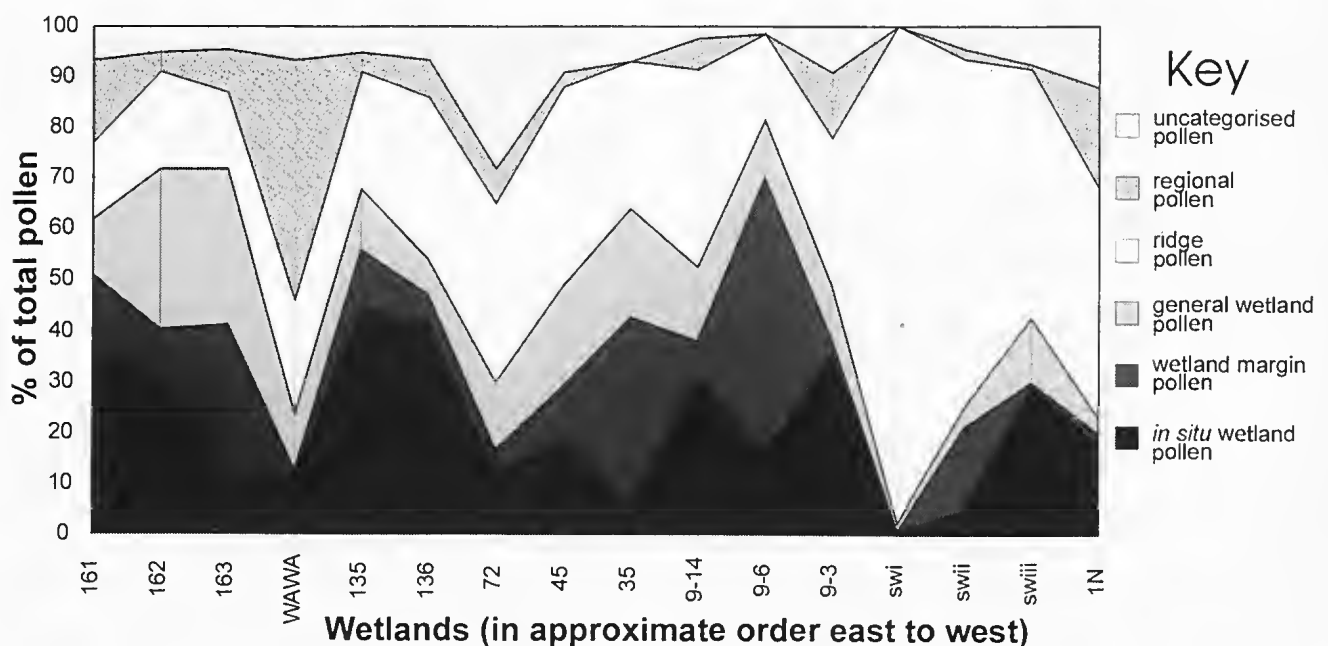
Figure 3. Composition of surface pollen for all sites.

Table 5

Comparison between extant vegetation and pollen abundance in surface. Categories used: a = abundant, *i.e.*, > 20%; p = present, *i.e.*, 5–20%; u = uncommon, *i.e.*, < 5%; ab = absent

Wetland basin	Species which are extant	Species abundance	Pollen abundance	Percentage of total pollen	Wetland basin	Species which are extant	Species abundance	Pollen abundance	Percentage of total pollen
161	*B. articulata*	a	p	5%	9-3	*B. juncea*	p	p	9%
	T. orientalis	p	p	12%		*I. nodosa*	p	a	21.5%
	C. asiatica	p	p	19%		*S. virginicus*	p	u	3%
	L. gladiatum	p	ab	0%		*M. rhaphiophylla*	u	u	4%
162	*M. teretifolia*	a	u	3%		*C. asiatica*	u	ab	0%
	C. asiatica	a	a	24%	9-6	*C. asiatica*	a	u	2.5%
	P. nodiflora	p	ab	0%		*B. juncea*	p	p	9%
	B. juncea	u	u	0.5%		*M. viminea*	p	u	1%
	S. virginicus	u	u	3%	9-14	*A. cyclops*	a	p	5.5%
163	*J. kraussii*	a	ab	0%		*J. kraussii*	p	ab	0%
	C. asiatica	p	p	10.5%		*B. juncea*	p	ab	0%
	B. juncea	p	u	1.5%		*S. virginicus*	p	p	6%
	S. virginicus	u	u	4%		*C. asiatica*	u	u	4%
WAWA	*B. articulata*	a	u	0.5%		*M. viminea*	p	p	15%
	T. orientalis	p	u	2%	swi	*L. gladiatum*	p	ab	0%
	M. viminea	p	u	0.5%		*J. kraussii*	p	ab	0%
	S. validus	u	ab	0%		*C. asiatica*	u	ab	0%
	C. asiatica	u	u	4.5%		*B. juncea*	u	u	1%
135	*M. rhaphiophylla*	a	p	15%	swii	*L. gladiatum*	p	ab	0%
	S. virginicus	a	a	29%		*J. kraussii*	p	ab	0%
	C. asiatica	p	ab	0%		*C. asiatica*	u	u	2.5%
136	*M. rhaphiophylla*	a	a	30%		*B. juncea*	u	u	2%
	C. asiatica	a	u	2%	swiii	*P. nodiflora*	a	u	0%
	S. virginicus	p	p	9.5%		*B. juncea*	p	u	0.5 %
72	*C. asiatica*	p	p	9%		*L. gladiatum*	p	p	5.5%
	B. juncea	p	u	0.5%		*C. asiatica*	p	ab	0%
	I. nodosa	u	u	2%		*J. kraussii*	p	ab	0%
45	*P. nodiflora*	a	u	1%		*S. validus*	p	p	14%
	C. asiatica	p	u	4.5%		*T. orientalis*	p	p	9%
	M. rhaphiophylla	p	p	13%	1N	*B. juncea*	a	ab	0%
	B. juncea	u	u	1%		*I. nodosa*	p	p	10%
	J. kraussii	u	ab	0%		*P. capitatum*	p	p	8%
35	*C. asiatica*	a	u	1%					
	M. rhaphiophylla	a	u	1.5%					
	M. cuticularis	p	u	2.5%					
	J. kraussii	p	ab	0%					
	P. nodiflora	u	u	1%					

orientalis, I. nodosa, and *C. asiatica,* were the most consistent contributors to the pollen assemblage (Fig. 4).

Pollen from species in the wetland margins was also differentially represented, with an abundance of *I. nodosa* pollen and a deficit of pollen from *X. preissii* and *A. saligna* (Fig. 4). For "ridge" pollen the most consistent contributors to the surface pollen were *O. axillaris* and species belonging to Chenopodiaceae (probably *Rhagodia baccata*), the latter being more abundant in wetlands nearest the coast where the plants are more numerous. Overall, the "regional" pollen was dominated

by species of Casuarinaceae (*Allocasuarina fraseriana, A. humilis*) and *Eucalyptus marginata,* important constituents of the *E. marginata/Banksia* spp. low woodland on the Spearwood Dune Ridge to the east.

Wetlands exhibited various amounts of pollen in the surface sediments. In order of abundance, the wetlands are listed in terms of total surface pollen per cm^3 of sediment, percentage of pollen from *in situ* wetland plants, and percentage of wetland pollen which was not autochthonous (Tables 6 & 7).

It can be seen that although wetland swi had the
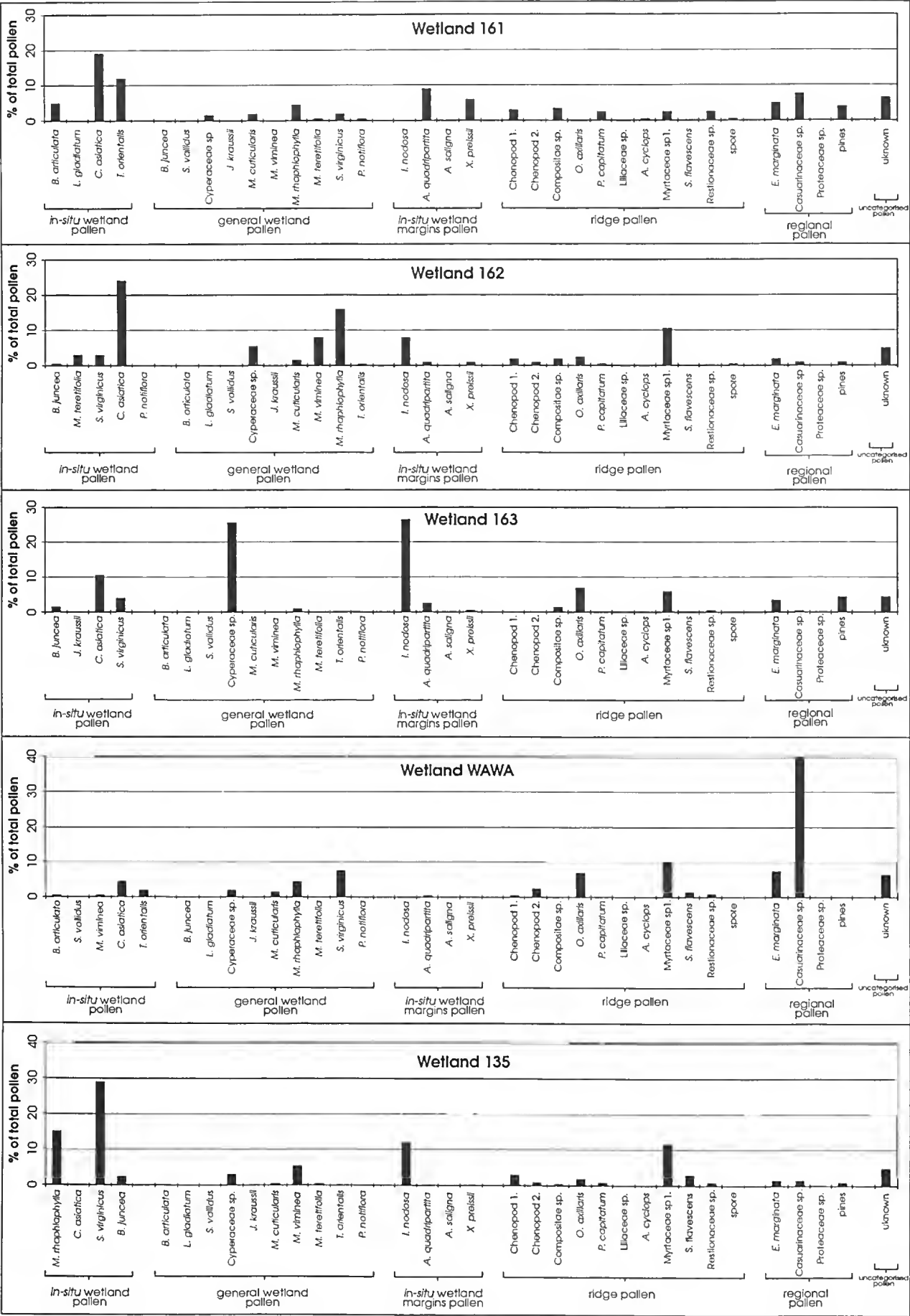
Figure 4. a,b,c,d: Graphs showing the surface pollen taxa, grouped according to the six categories, plotted as a percentage of total pollen.

Wetland swii
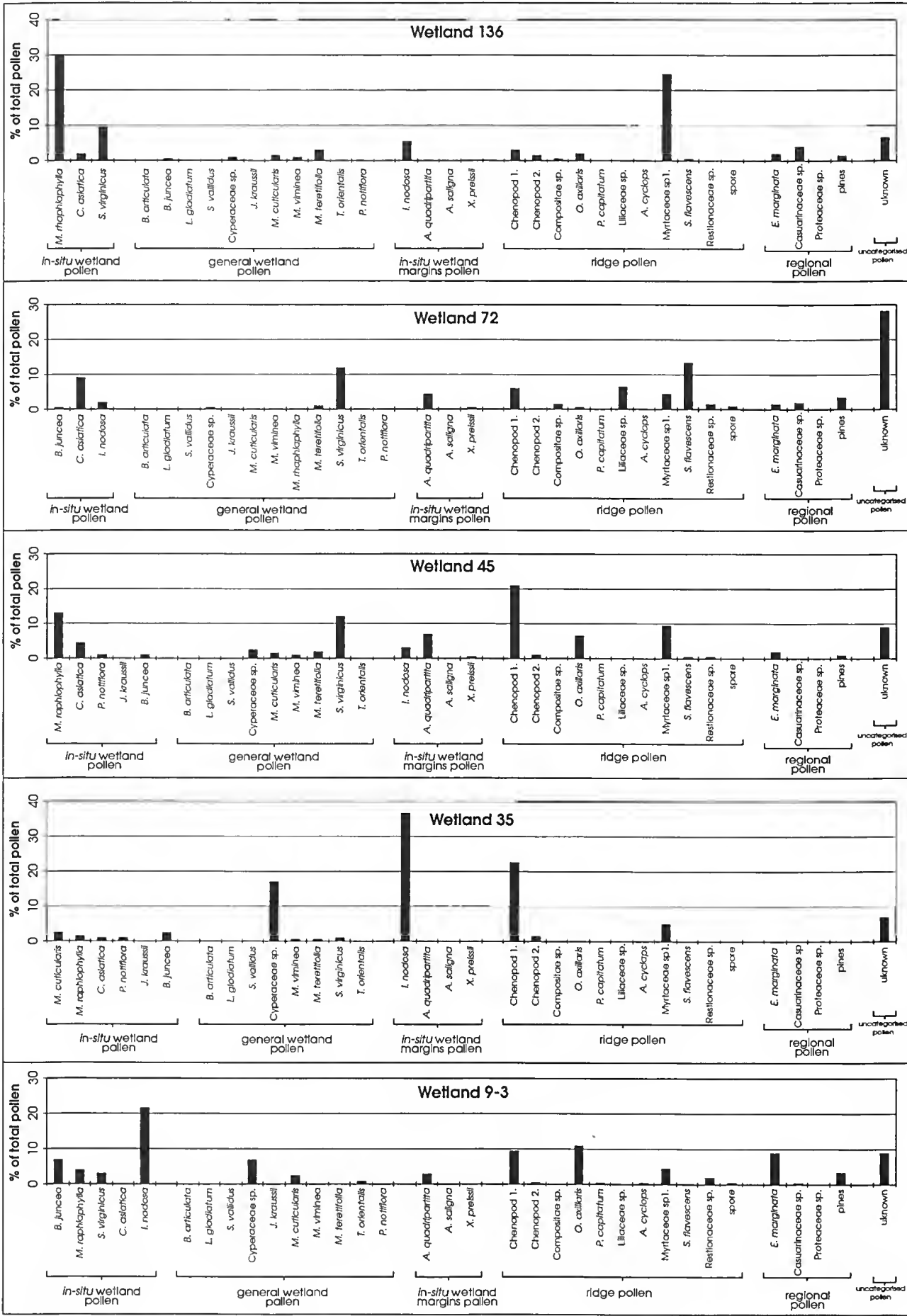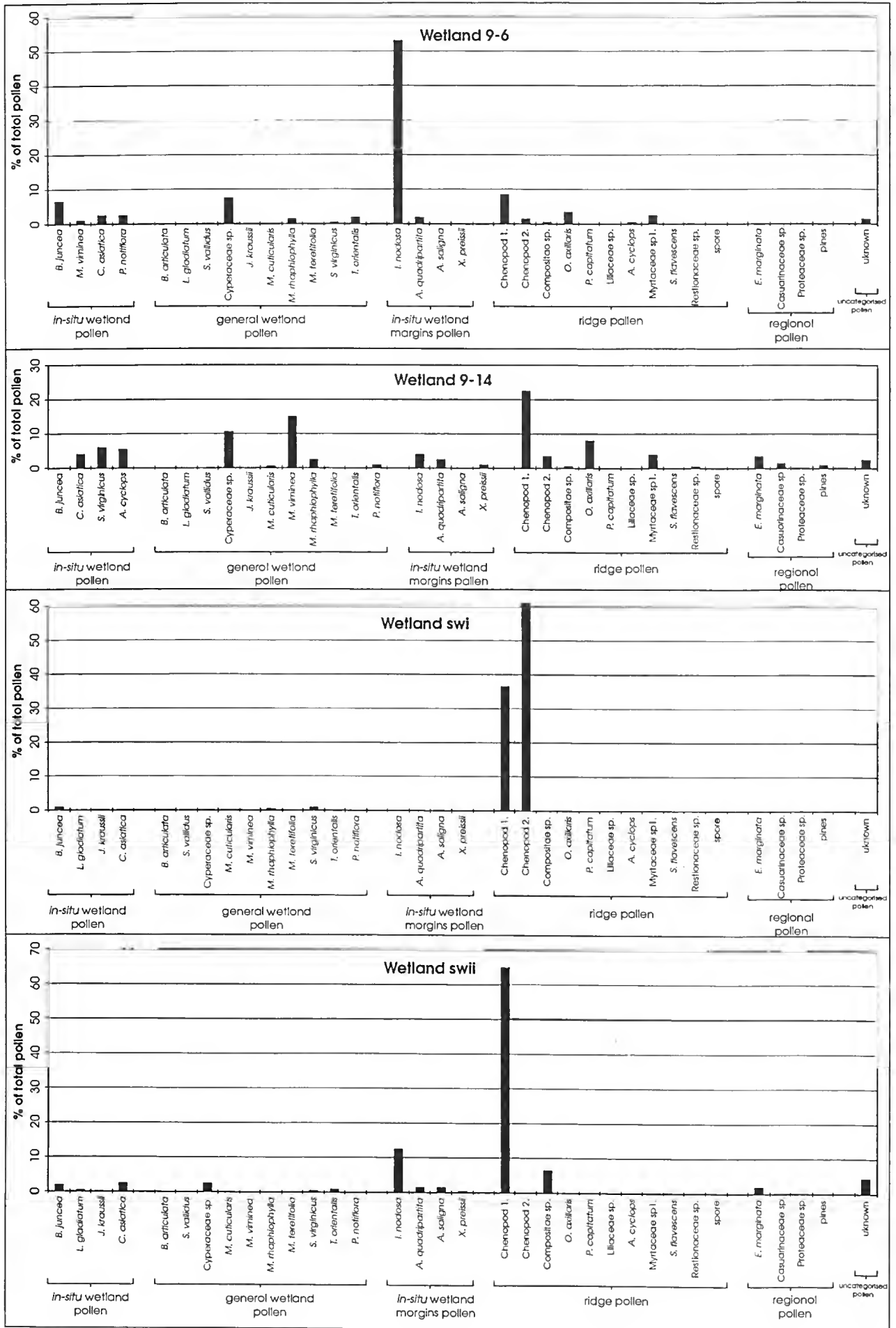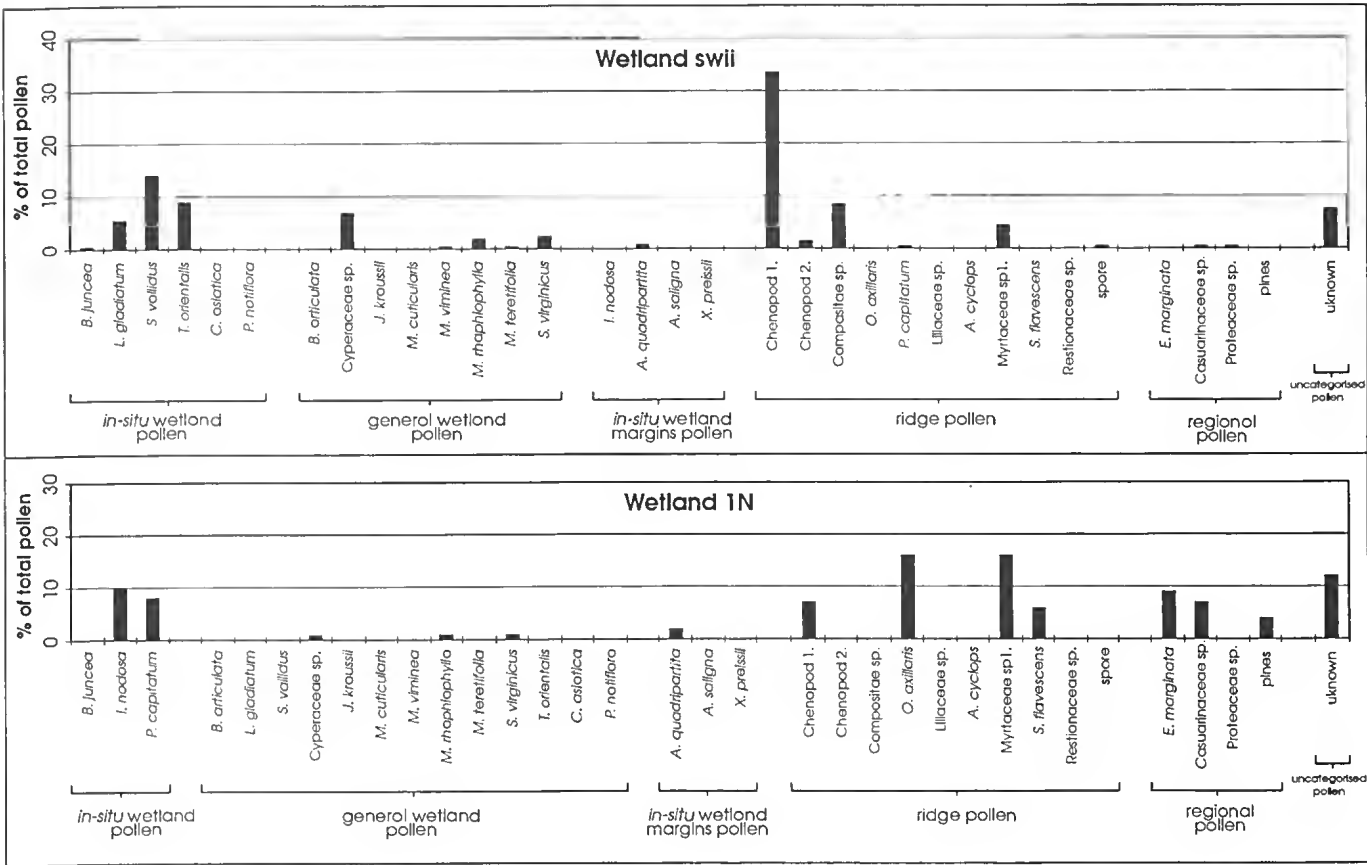
Wetland 1N

Table 6

Wetlands in order of decreasing pollen abundance in the surface sediments

Wetlands	Total pollen counts/cm³ (rounded to nearest 500)
swi	907,000
35-4	91,000
swii	88,000
9-6	81,000
45	47,000
135	40,000
136, swiii	35,000
9-3	34,500
161	34,000
9-14	31,000
163	29,000
72, 162	29,000
WAWA	26,000
1N	6,000

highest number of pollen per cm³ of sediment, the component of wetland pollen was minimal (Table 7). Wetland 162, in contrast, had much lower numbers of pollen grains per cm³ of sediment, but the proportion of wetland pollen was greater. Apart from wetland swi which was dominated by "ridge" pollen, many of the wetlands had very similar pollen densities in the surface sediments, *e.g.*, wetlands 135, 136, 9-3, 161, 9-14, swiii. The percentage of pollen derived from *in situ* wetland vegetation was more variable and is governed by a number of factors, some of which are: size of wetland;

ratio of cover of high pollen producing plants to low pollen producing plants; number of adjacent wetlands; proximity of adjacent wetlands; and height of basin floor relative to surrounding ridges. The low numbers of pollen grains from *in situ* wetland species in wetlands swi and swii can be explained in terms of the factors listed above. These wetlands are very small, with minimal elevation difference between basin floor and adjacent ridges, and a high proportion of low pollen producing plants.

Use of surface pollen assemblages in interpreting fossil wetland pollen sequences

Autochthonous vs allochthonous assemblages

Separating autochthonous pollen assemblages from proximal allochthonous assemblages and from distal allochthonous assemblages is an important consideration when pollen is to be used to interpret fossil wetland pollen sequences.

In most wetlands, the major component of surface pollen deriving from wetland vegetation was autochthonous. There were exceptions in three wetlands, *viz.*, 163, 35 and 72. In wetlands 163 and 35, where *J. kraussii* is present, the discrepancy probably was caused by the absence of *J. kraussii* pollen, and in wetland 72 by very low numbers of *B. juncea* pollen.

The major component of pollen derived from upland vegetation was from ridges adjacent to wetlands. This pollen was particularly numerous in wetland basins in the shallower swales which are also the youngest of the wetlands, *e.g.*, wetlands swi, swii, and 1N. In wetland

Table 7

Wetlands listed in order of decreasing pollen abundance in surface sediments from wetland species. (Key to species: Ac = *A. cyclops*, Ba = *B. articulata*, Bj = *B. juncea*, Ca = *C. asiatica*, In = *I. nodosa*, Lg = *L. gladiatum*, Mc = *M. cuticularis*, Mr = *M. rhaphiophylla*, Mt = *M. teretifolia*, Pc = *P. capitatum*, Scv = *S. validus*, Sv = *S. virginicus*, To = *T. orientalis*)

Wetlands	*In situ* wetland pollen as percentage of total pollen	Main species in pollen assemblage	Percentage of allochthonous wetland pollen	Total pollen counts/cm³ (rounded to nearest 500)
135	44	Sv, Mr	12	40,000
136	41.5	Mr, Sv	7	35,000
161	36	Ca, To, Ba	11	34,000
9-3	35.5	In, Bj, Mr	10.5	34,500
162	30.5	Ca, Mt, Sv	31.5	29,000
swiii	29	Scv, To, Lg	12.5	35,000
45	18.5	Mr, Ca	20	47,000
1N	18	In, Pc	3	6,000
9-14	15.5	Sv, Ac, Ca	14.5	31,000
9-6	15	Bj	11.5	81,000
163	12	Ca, Sv	30.5	29,000
72	11.5	Ca	13.5	29,000
WAWA	7.5	Ca	15.5	26,000
35	6	Mc	21.5	91,000
swii	5	Ca, Bj	4	88,000
swi	1	Bj	1.5	907,000

WAWA, which was the exception, the major component of the pollen derived from upland vegetation was regional pollen, probably because of the impedance effect of the higher than normal eastern ridge that borders the wetland. The high proportion of locally derived pollen on the Becher cuspate foreland is largely due to its geometry and configuration. The Rockingham Coastal Plain is a regionally prominent projecting feature along the coast. It lies between the Indian Ocean and mainland, where local wind and rain patterns differ slightly from the rest of the mainland (C A Semeniuk 2006). At the scale of the cuspate foreland, the topography is low and unlikely to interrupt the regional aeolian transport onshore and offshore. At the small scale, within the swales, wind is typically of low frequency and low velocity.

Interpreting fossil wetland pollen sequences

Whether pollen of wetland vegetation is *in situ*, derived from the wetland margins, or transported by wind to a particular basin from other proximal or distal basins, is a critical consideration in reconstructing vegetation history from the pollen record. While transported pollen preserved in the stratigraphic profile may reflect the long-term regional and sub-regional species pool, it cannot be used to reconstruct comparative vegetation history of individual wetlands. Difficulties in interpretation of the pollen record also will arise when the occurrence of a given species is the result of *in situ* production and wind transport.

Baumea articulata and *L. gladiatum* pollen appear to be reflecting *in situ* production and accumulation. The occurrences of pollen of *M. rhaphiophylla*, *M. viminea*, *M. teretifolia*, *M. cuticularis*, *Typha* sp., *S. virginicus*, and *C. asiatica* at first appearances would seem to be related in varying degrees to *in situ* production and contribution from wind. In an attempt to resolve this problem, the occurrences of the four species of *Melaleuca* in the study area, and the distribution of their pollen in surface

sediment were explored further (Fig. 5). The patterns for the four *Melaleuca* species show that abundant pollen for a given species occurs in the surface sediment where that species is currently growing. For instance, the highest numbers of pollen of *M. rhaphiophylla* are in wetlands 135, 136, and 45, where the species is common, and similarly, there are high numbers of pollen of *M. cuticularis* in wetland 35 where that species is present. In wetlands where *M. teretifolia* and *M. viminea* are present today, there are also relatively high numbers of their pollen, although in this case other wetlands exhibit a higher abundance.

There is also some indication of the effect of wind in transporting pollen using *Melaleuca* as a signature. For instance, there is a high proportion of pollen of *M. cuticularis* in the wetlands near wetland 35, signalling wind transport of this pollen from its source in wetland 35 to nearby basins by landbreezes and seabreezes, and none in wetlands further west, *viz.*, wetlands swi, swii, swiii, and 1N (Fig. 5). Further, there is a high proportion of pollen of *M. viminea* in the wetlands near wetland 9-6 and 9-14, signalling wind transport of this pollen from its source to nearby basins such as wetlands 45 and 35 by landbreezes and seabreezes. The occurrences of pollen of *M. rhaphiophylla*, *M. teretifolia* and *M. viminea* in wetland swiii, while absent in adjacent near-coastal wetlands along this same beachridge swale (*viz.*, swi, swii, and 1N) illustrate the localised nature of wind delivery of pollen by landbreezes.

While there appears to be a relationship between an extant species and high counts of their pollen in surface sediments, and the occurrence of high pollen counts of some species due to wind transport, there are variations. Wind transport does not explain several examples of high counts of pollen where the species do not occur today: *M. rhaphiophylla* in wetlands 161, 162, and 163, *M. teretifolia* in wetlands 136 and 45, and *M. viminea* in wetlands 162 and 135 (Fig. 5). This would suggest that these species have come and gone over the period of
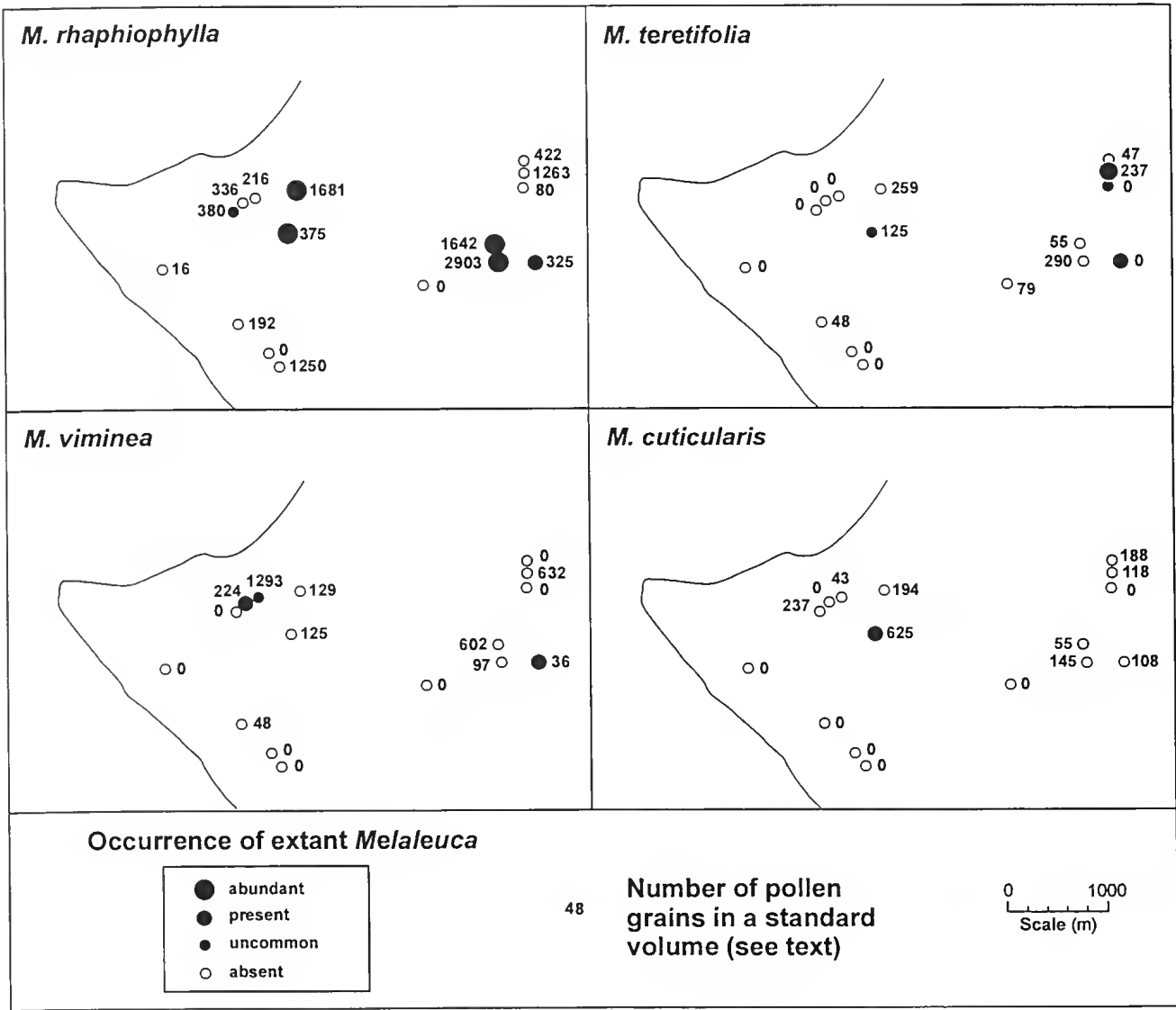
Figure 5. Occurrence of extant *Melaleuca* species in the wetland basins, noted in terms of relative abundance, and the abundance of their pollen in a standard volume of surface sediment (see text).

several decades or centuries, and that their pollen in the upper centimetre of sediment records these former populations.

Similarly, the distribution of *S. virginicus* pollen provides insight into the resolution of autochthonous *versus* wind derived pollen. The pollen is relatively widespread but does not occur throughout all wetland basins. *S. virginicus* tends to be an understorey component to shrubs such as *M. viminea*, the canopy of which largely precludes the dispersion of its pollen by wind.

A measure of the contribution of wind in supplying pollen from wetland species to a given basin was explored using the occurrence of the pollen of upland species, as these species definitively indicate an origin outside of the wetland basin (Fig. 6). The effect of wind in delivering upland pollen was explored using the distributions of three species of regional and sub-regional pollen with distinct distal sources to ascertain the contribution by easterly and westerly winds. *Olearia axillaris* is a primary dune species restricted to near coastal locations. Its pollen would have to be delivered by westerly wind to the wetlands. Casuarinaceae spp. and *E. marginata* pollen derive from the Spearwood Dune Ridge and further eastward, and have to be delivered by easterly winds. The abundance of *O. axillaris*, Casuarinaceae spp., and *E. marginata* in the surface pollen varies from basin to basin, even for basins close to each other. There is no clear gradient in abundance from source to distal wetland. For example, for Casuarinaceae spp., adjacent wetlands 161, 162, 163, register 703, 79, and 40 pollen grains, respectively, and nearby wetland 9 shows spatial variation from 0 to 129. The patterns show different wind fields and different grain fallout for a single taxon, and between taxa in an essentially isochronous layer, *i.e.*, the surface sediment of the wetland in a coastal climatic setting of today, and illustrate a wide variation in abundance across the receiving depositional surface. The study of the three upland pollen types suggests that using upland pollen abundance in isolation as an indicator of wind intensity and possible climatic changes, without supplementary information on pollen aerodynamics, pollen production
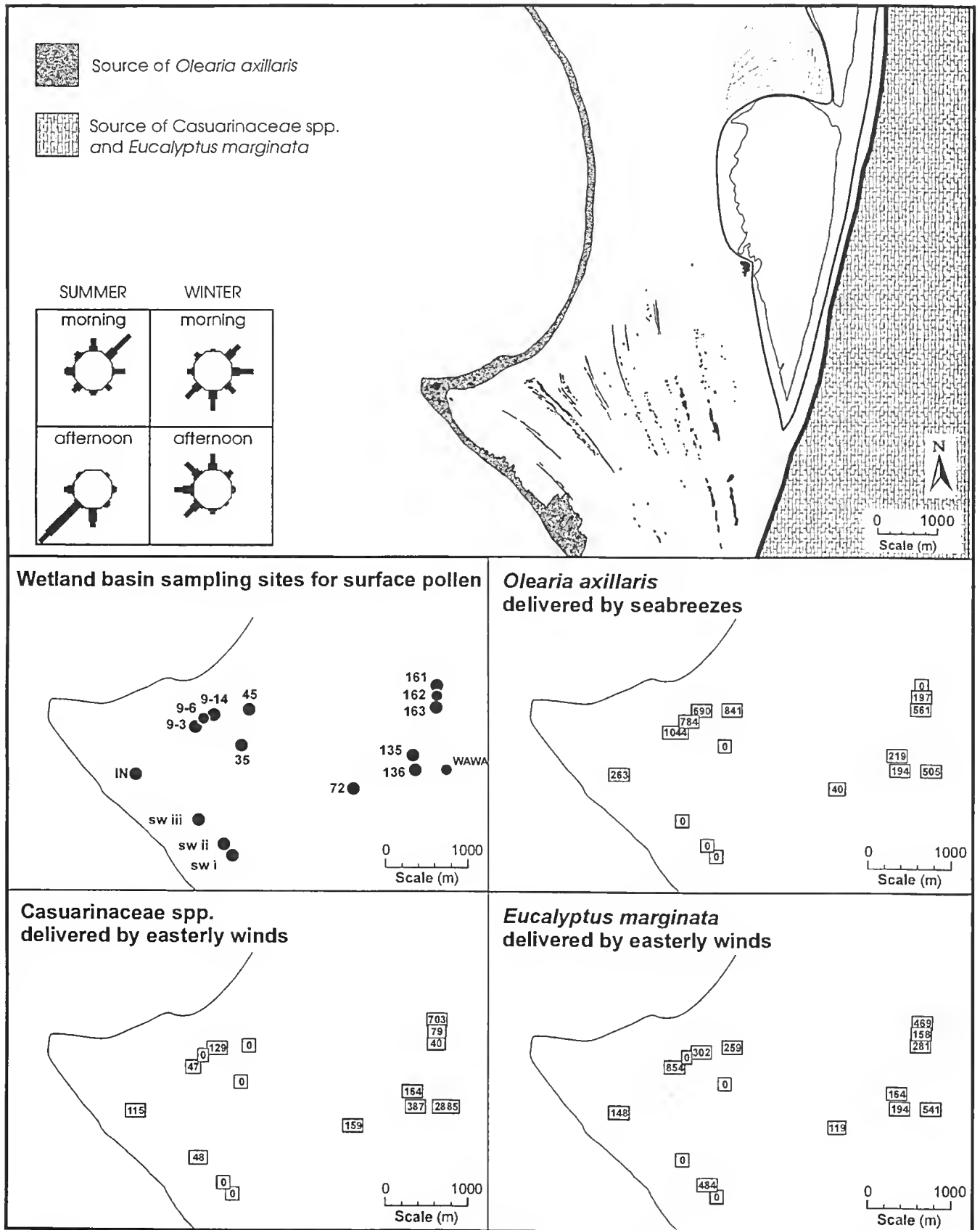
Figure 6. Sources of the three types of upland pollen (*viz.*, *O. axillaris*, *E. marginata*, and Casuarinaceae spp, with source being coastal, and inland regional, respectively), summary of wind delivery systems shown as wind roses for summer and winter, and abundance of these pollen in the surface sediments of the wetlands (boxed numbers refer to number of pollen within a standard volume; see text). The regional sources for *E. marginata* include that shown in the Figure (the Spearwood Dunes), as well as sources further east, such as the Bassendean Dunes and the Darling Plateau.

rates, abundance and location of source material, and wind currents, is problematic. The only conclusion that can be reached, if regional pollen occurs within a wetland basin within the Becher Suite, is that it is exogenic, and that for diagnostic taxa, it derives from easterly or westerly sources. The information in Figure 6 even suggests that the absence of diagnostic species of distal regional pollen within a given wetland basin cannot be used as an indicator of wind patterns.

It is concluded that the pollen of the main species of wetland plants forms *in situ* accumulations. With a baseline relationship established between extant wetland vegetation, subregional vegetation patterns, and regional vegetation patterns, the information in this paper can be used to construct the history of vegetation in wetlands of the Becher Point area, the subject of a later paper (C A Semeniuk, Milne, Ladd & Semeniuk, unpublished manuscript).

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Genetic diversity of *Rhagada* land snails on Barrow Island

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Abstract

The dominant group of land snails in the Pilbara Region is the camaenid genus *Rhagada*, which includes several species confined to islands. Analysis of allozymes confirmed the presence of two genetically distinct species of *Rhagada* on Barrow Island: a small species restricted to the northern tip of the island, and a large species widespread over the remainder of the island. Comparisons amongst 19 samples of the widespread, large species revealed distinct populations, but with unusually low levels of genetic subdivision, and no detectable geographic pattern on the island. In contrast with the low divergence within species, the two species are genetically the most distinctive of all species of *Rhagada* examined from the Pilbara Region. The genetic distinctiveness of these species highlights the conservation value of Barrow Island for these endemic snails, and raises questions of the evolutionary history of *Rhagada* in the Pilbara Region.

Keywords: *Rhagada*, genetic diversity, land snails, Barrow Island

Introduction

Islands are of special interest in the context of evolution and, increasingly, conservation. Genetic studies have found divergent populations of mammals (*e.g.*, Schmitt 1978; Moro *et al.* 1998; Eldridge *et al.* 1999; Sinclair 2001; Hinten *et al.* 2003) and reptiles (*e.g.*, Sarre *et al.* 1990) on isolated Australian islands. In addition to facilitating genetic divergence, islands are important refugia and play a special role for conservation of terrestrial fauna in Western Australia.

In both evolutionary and conservation contexts, there has been a strong focus on vertebrate species. Terrestrial invertebrates, on the other hand, often have less capacity for dispersal and hence smaller geographic distributions than species of vertebrates (*e.g.*, Harvey 2002). Limited dispersal and narrow distributions increase both the likelihood of locally distinct genetic forms and their vulnerability to extinction. Land snails are well recognised for their limited vagility and often small distributions, but have been poorly studied compared with vertebrates (*e.g.*, Ponder 1997). To illustrate, Ponder (1997) pointed out that there are more than 900 species of terrestrial molluscs in Australia, with the actual total probably being closer to 2000, but he could find only three genetic studies of native species (Hill *et al.* 1983; Woodruff & Solem 1990; Daniell 1994). We know of only four subsequent genetic studies (Clarke & Richardson 2004; Hugall *et al.* 2002, 2003; Johnson *et al.* 2004).

In the Pilbara Region, the dominant group of land snails is the genus *Rhagada*, which is endemic to northern Western Australia (Solem 1997). Although mainland species in the Pilbara Region tend be distributed over hundreds of kilometres, there are unique species restricted to islands in the Dampier Archipelago and the Montebello Islands group (Solem 1997). There appear to be two species of *Rhagada* on Barrow Island (Slack-Smith 2002), the smaller species being approximately 10 mm diameter and the larger species approximately 20 mm diameter (Fig. 1). These species have not been taxonomically described or assigned to any species. The small species has been found only on the northern end of Barrow Island (Slack Smith 2002), although its shells closely resemble those of *R. plicata*, which Solem (1997) reported from the nearby Montebello Islands. The larger species is abundant and widespread over the rest of Barrow Island. In their physiological study, Withers *et al.* (1997) referred to this latter species as *R. tescorum*, a mainland species, but its similarity to both mainland *R. capensis* and *R. convicta* and to the Dampier Archipelago species *R. perprima* emphasises the taxonomic difficulties of this genus (Slack-Smith 2002).
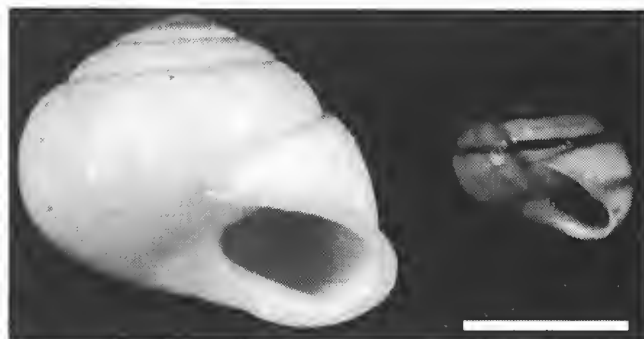
Figure 1. Representative shells of the large and small species of *Rhagada* on Barrow Island. Scale bar = 1 cm.

In this study, allozyme electrophoresis was used to examine genetic diversity of *Rhagada* on Barrow Island, to answer questions at four levels:

(a) Are the two apparent (morphologically distinct) species on Barrow Island genetically distinct? Snail shells can vary greatly among populations of the same species (*e.g.*, Johnson *et al.* 1993; Johnson & Black 2000). Consequently, shell morphology alone may not be reliable for differentiating the two species of *Rhagada*. Independent genetic evidence for species distinctness is, therefore, important for evaluating the relationships of the small and large forms.

(b) Are the species on Barrow Island genetically unique? Unusually high levels of genetic similarity have been found among species of *Rhagada* on the mainland and in the Dampier Archipelago (Johnson *et al.* 2004). Comparison of the species on Barrow Island with those from other parts of the Pilbara Region will determine whether the island species are unique.

(c) How much genetic divergence is there among populations of the widespread, larger species on Barrow Island and what is the geographic pattern of that divergence?

(d) At the smaller scale, are there genetically distinct groups of populations?

This is the first study of local genetic subdivision within a species of *Rhagada*.

Methods

Samples

Live, adult *Rhagada* were collected between March and July 2004, at 21 sites across Barrow Island, providing a good coverage of the island (Fig. 2). Two samples of the small species were collected from the northern portion of the island, and 19 samples of the large species were collected from widely dispersed sites across the island. Sampling sites are superimposed on the vegetation map of Buckley (1983) in Figure 2.

In the laboratory, the snails were activated overnight, by placing them on moist tissue paper in sealed plastic boxes, and were then frozen at -80°C, pending allozyme electrophoresis. This ensured that the processed snails were alive and active.

Allozyme electrophoresis

Preparation of samples and allozyme electrophoresis followed the procedures used in a previous study of *Rhagada* from the Pilbara mainland and Dampier Archipelago (Johnson *et al.* 2004). Thirteen enzymes, representing 15 gene loci, were successfully examined: adenylate kinase (EC 2.7.4.3; *Ak* locus); arginine phosphokinase (EC 2.7.3.3; *Apk*); glucosephosphate isomerase (EC 5.3.1.9; *Gpi*); isocitrate dehydrogenase (EC 1.1.1.42; *Idh1* and *Idh2*); lactate dehydrogenase (EC 1.1.1.27; *Ldh*); leucine amino peptidase (EC 3.4.-.-; *Lap*); leucyl-glycylglycine peptidase (EC 3.4.-.-; *Pep-lgg*; TEB); leucyl-leucine peptidase (EC 3.4.-.-; *Pep-ll*); leucyl-tyrosine peptidase (EC 3.4.-.-; *Pep-lt*); valyl-leucine peptidase (EC 3.4.-.-; *Pep-vl*); phosphoglucomutase (EC
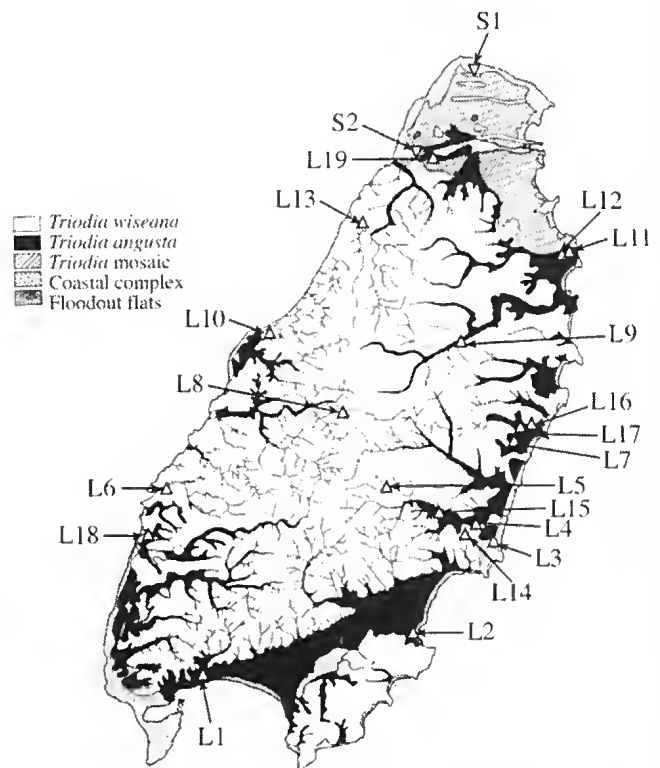
Figure 2. Sample sites of *Rhagada* on Barrow Island. L = large species; S = small species. Vegetation map from Buckley (1983).

5.4.2.2; *Pgm1* and *Pgm2*); phosphogluconate dehydrogenase (EC 1.1.1.43; *Pgd*); and superoxide dismutase (EC 1.15.1.1; *Sod*). Multiple loci for a particular enzyme and allozymes at each locus were labelled according to relative electrophoretic mobility.

Samples were processed in two stages. First, four snails from each site were examined for all fifteen loci. Both the large and the small species were included, providing genetic comparison between the two apparent species on Barrow Island. In addition, a sample of *Rhagada convicta* (the most widespread species on the mainland) from Mundabullagana Station (20° 08' 09.7" S, 118° 01' 31.0" E) was included. Because the species examined so far are all very similar for their allozymes, this sample provided an adequate link to the published genetic comparisons among all known species of *Rhagada* from the Pilbara mainland and most of the species from the Dampier Archipelago (Johnson *et al.* 2004), placing the species from Barrow Island in the broader geographic context.

In addition to determining whether the species on Barrow Island are genetically distinct, this first stage of electrophoresis determined which enzymes were genetically variable in the large, widespread species on Barrow Island. These variable enzymes were then examined in larger samples of this species from all 19 sites. Five sites (L14-17, L19 in Fig. 1) were represented by small samples (10–11 snails), while the other 14 sites had more reliable samples of 33 to 52 snails.

Analysis of data

Allelic frequencies were calculated at each locus, and differences between populations were measured over all 15 loci as Nei's (1978) genetic distance. The matrix of

genetic distances was summarized by a UPGMA phenogram, using PHYLIP version 3.64 (Felsenstein 1993). The phenogram was illustrated with the help of TreeView (Page 1996). This analysis included all 21 samples from Barrow Island and the species of *Rhagada* from the Pilbara mainland and the Dampier Archipelago (Johnson *et al*. 2004).

For the variable loci in the large species on Barrow Island, genetic subdivision among all 19 samples was measured as Wright's fixation index, F_{ST}, using GENEPOP (Raymond & Rousset 1995), as implemented on the web (http://biomed.curtin.edu.au/genepop). F_{ST} is the proportion of genetic variation due to differences between populations. The statistical significance of genetic differences among populations was tested by randomization contingency tests, using GENEPOP. Differences between pairs of sites were measured as pairwise F_{ST}. Pairwise F_{ST} was also plotted against geographic distance between sites, to determine whether there was a pattern of isolation by distance. The significance of the association of genetic distance with geographic distance was tested with a Mantel test, using GENEPOP.

Results

Comparisons between species

The genetic comparisons confirmed the distinctness of the large and small species of *Rhagada* on Barrow Island. The two species are completely different at the *Ldh*, *Pgd* and *Pgm1* loci and have very divergent frequencies of

alleles at the *Gpi*, *Idh1* and *Pep-vl* loci (Table 1). The average genetic distance between the two species was 0.34. Although not unusually divergent for congeneric species, the Barrow Island species are genetically the most distinctive of those tested so far in this region. The phenogram illustrates the distinctness of the Barrow Island *Rhagada* from the species on the Pilbara mainland and the Dampier Archipelago (Fig. 3). The large species on Barrow Island clusters with the group of species from the mainland and the Dampier Archipelago, but is distinguished by fixation of the unique *Ldh^111* allele. The small species is well separated from all the other species, in its own cluster.

Spatial variation within the large species

The phenogram also illustrates the high degree of similarity of populations within each of the species on Barrow Island. Further genetic analysis was conducted on the widespread, large species, to determine the amount and pattern of genetic divergence across the island. Only three of the 15 allozyme loci had multiple alleles in this species. At two of these (*Gpi* and *Pgm1*), one allele predominated in all sites, with alternative alleles occurring at frequencies < 0.1 at many sites (Table 1). Only the *Idh1* locus was consistently polymorphic, with the less common *Idh1^100* allele having frequencies of 0.112 to 0.404 among the 19 sites. Based on these three variable loci, the level of genetic subdivision across the island was small, with an overall F_{ST} of 0.023. Nevertheless, although the subdivision was modest, it was statistically significant ($P < 0.01$) for each of the three loci, indicating that populations are locally independent.

Table 1

Allelic frequencies at variable gene loci in samples of *Rhagada* species from Barrow Island. N = sample sizes for *Gpi*, *Idh1* and *Pgm1*; for other loci, sample sizes were four individuals. The nine invariant loci examined are not shown.

Site	N	*Gpi* 152	100	52	*Idh1* 100	91	*Ldh* 111	100	*Pep-vl* 100	95	*Pgd* 100	67	*Pgm1* 144	111	100	78
Large species																
L01	33	0.045	0.894	0.061	0.303	0.697	1.000	...	1.000	...	1.000	...	...	...	1.000	...
L02	40	0.025	0.975	...	0.138	0.863	1.000	...	1.000	...	1.000	...	0.062	...	0.938	...
L03	40	...	1.000	...	0.262	0.738	1.000	...	1.000	...	1.000	...	0.025	...	0.975	...
L04	40	0.013	0.913	0.075	0.363	0.637	1.000	...	1.000	...	1.000	...	...	...	1.000	...
L05	48	...	0.938	0.062	0.229	0.771	1.000	...	1.000	...	1.000	...	0.010	...	0.990	...
L06	40	...	1.000	...	0.389	0.611	1.000	...	1.000	...	1.000	...	...	...	1.000	...
L07	30	...	1.000	...	0.350	0.650	1.000	...	1.000	...	1.000	...	0.017	...	0.983	...
L08	40	...	0.988	0.013	0.112	0.887	1.000	...	1.000	...	1.000	...	0.025	...	0.975	...
L09	40	...	0.925	0.075	0.375	0.625	1.000	...	1.000	...	1.000	...	0.025	...	0.975	...
L10	36	...	0.972	0.028	0.278	0.722	1.000	...	1.000	...	1.000	...	...	...	1.000	...
L11	40	...	0.925	0.075	0.262	0.738	1.000	...	1.000	...	1.000	...	0.062	...	0.938	...
L12	48	...	0.969	0.031	0.302	0.698	1.000	...	1.000	...	1.000	...	0.083	...	0.917	...
L13	40	...	0.950	0.050	0.325	0.675	1.000	...	1.000	...	1.000	...	0.062	...	0.938	...
L14	11	...	0.955	0.045	0.227	0.773	1.000	...	1.000	...	1.000	...	...	...	1.000	...
L15	11	0.045	0.864	0.091	0.136	0.864	1.000	...	1.000	...	1.000	...	...	...	1.000	...
L16	10	...	0.950	0.050	0.150	0.850	1.000	...	1.000	...	1.000	...	...	...	1.000	...
L17	10	...	1.000	...	0.300	0.700	1.000	...	1.000	...	1.000	...	...	...	1.000	...
L18	52	0.048	0.952	...	0.404	0.596	1.000	...	1.000	...	1.000	...	...	...	1.000	...
L19	10	...	0.950	0.050	0.200	0.800	1.000	...	1.000	...	1.000	...	...	...	1.000	...
Small species																
S20	4	0.500	0.500	...	...	1.000	...	1.000	0.500	0.500	...	1.000	...	1.000	...	...
S21	4	1.000	...	...	...	1.000	...	1.000	0.375	0.625	...	1.000	...	0.875	...	0.125
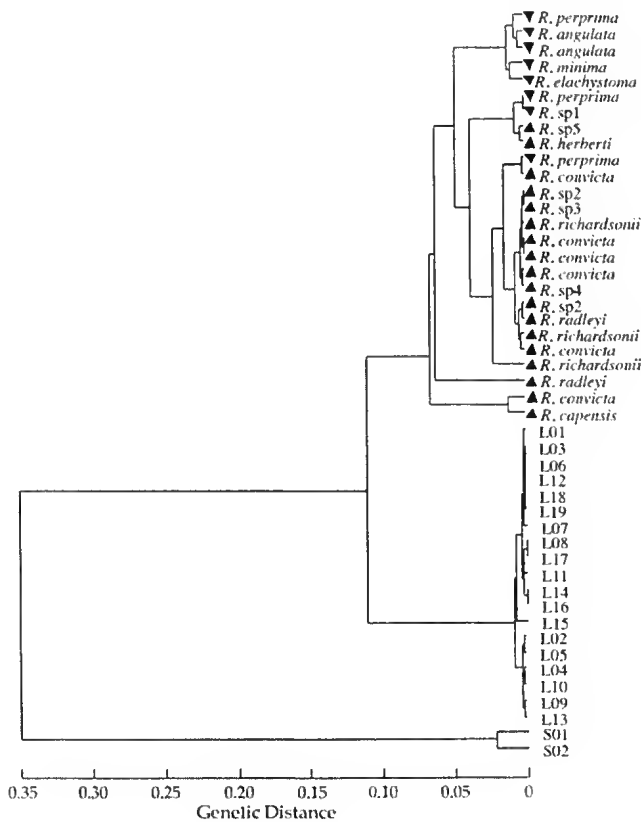
Figure 3. UPGMA phenogram of genetic distances among populations of the two species of *Rhagada* on Barrow Island and species on the Pilbara mainland (upright triangles) and Dampier Archipelago (inverted triangles). Site codes for Barrow Island as in Fig. 1 (small species = S01 to S02; large species = L01 to L19)

Figure 4. Frequencies of the *Idh1¹⁰⁰* (shaded segments) and *Idh1⁹¹* (white segments) alleles in samples of the large species of *Rhagada*. Small circles = small samples.

Allelic frequencies at the *Idh1* locus showed no obvious geographic pattern across the island (Fig. 4). Similarly, the rarer alleles at the less polymorphic *Gpi* and *Pgm1* loci were scattered across the island (Table 1). Consistent with this apparent lack of geographic pattern, there was also no association of genetic divergence and geographic distance across the island ($r = 0.01$, $P > 0.8$, Mantel test). This analysis included the five small samples, as well as the 14 large samples, but removal of the small samples had no effect on the search for spatial pattern.

Discussion

These genetic comparisons confirm the occurrence of two morphologically and genetically distinct species of *Rhagada* on Barrow Island. Co-occurrence of species of *Rhagada* is extremely rare (Solem 1997; Johnson *et al.* 2004). The two species on Barrow Island fit this general pattern, with complementary distributions. These distributions reflect the distribution of contrasting habitats on the island. The northern end of the island, occupied by the small species, has a mosaic of *Triodia* species (Buckely 1983), and the smaller species of *Rhagada* was collected from flat hummock grasslands, whereas the widespread, larger species was found predominantly in and near ravines dominated by *Triodia angusta*, which are common outside the northern end of the island. Because the two species were not found

together, we do not have direct evidence of intrinsic reproductive isolation. Nevertheless, the species were found within 0.8 km of each other, and the genetic differences were consistent throughout the distributions of both types, confirming that they are separate species.

These are the two most genetically divergent species of *Rhagada* so far examined in the Pilbara Region. Indeed, comparisons amongst all species of *Rhagada* on the Pilbara mainland did not reveal unique alleles in any of them (Johnson *et al.* 2004). In addition to highlighting the conservation significance of these endemic snails on Barrow Island, the genetic distinctiveness of the two species raises questions about the evolutionary radiation of *Rhagada*. The large species on Barrow Island is apparently closely related to the species on the Pilbara mainland and the Dampier Archipelago. In contrast, the small species apparently represents a distinct lineage, with no counterparts yet identified on the mainland. Its shells fit Solem's (1997) description of *R. plicata* on the nearby Montebello Islands, a species that has not yet been examined genetically. Although not recorded by Solem (1997), a large species, similar to that on Barrow Island, also occurs in the Montebellos (P. Kendrick, personal communication). Although the shells of the large species are very similar to those of several mainland species, the small species has shells unlike any described species from the Pilbara mainland. Instead, they are similar in

shape and sculpture to the shells of *R. dringi*, from 80-mile Beach. This raises the possibility of two lineages from the north leading to the colonization of Barrow Island and the Montebello Islands, only one of which diversified in the mainland Pilbara Region. More extensive phylogenetic analyses, using more sensitive molecular markers are needed to test this hypothesis.

In contrast with the substantial genetic divergence between the two species of *Rhagada* on Barrow Island, little genetic divergence was found among populations of the widespread, large species. The small genetic differences were statistically significant, however, indicating that populations are locally independent, as is typical of land snails. On the mainland, for example, demographically independent populations of *R. capensis* span less than 40 m (Johnson & Black 1991), well below the scale of resolution of the present study.

Despite independence of local populations, the level of genetic subdivision of the large species on Barrow Island over distances of up to 20 km is exceptionally low for a land snail (e.g., Johnson 1976; Johnson *et al.* 1993; Davison & Clarke, 2000; Arnaud *et al.*, 2003). The frequencies of the common alleles at the *Idh1* locus show only modest variation across the island, and even the relatively uncommon alleles at the *Gpi* and *Pgm1* loci are widespread and are not restricted to particular portions of the island. Although additional genetic markers would be desirable, the genetic patterns within the large species of *Rhagada* on Barrow Island give no indication of geographic areas with genetically distinct populations. The low level of subdivision, combined with the lack of clear spatial pattern, suggests at least occasional gene flow across the whole island, perhaps facilitated by extreme wet periods during cyclonic rain.

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Cyanobacterial Blooms in the Wetlands of the Perth region, Taxonomy and Distribution: an Overview

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Abstract

The distribution pattern (spatial and temporal) of cyanobacterial blooms in Perth wetlands and the Canning River in Western Australia has been investigated sporadically over a span of 20 years. The major bloom-forming species have been identified as *Microcystis aeruginosa, M. flos-aquae, Anabaena circinalis, A. spiroides* and *Nodularia spumigena*. Blooms of potentially toxic *Anabaena* spp. have occurred in the Canning River since 1993, and in many Perth wetlands for several years. For the first time, the Swan River estuary itself experienced a prolonged toxic bloom of *Microcystis flos-aquae* in February 2000. The two species of *Anabaena* and *Microcystis aeruginosa* blooms have occurred under salinity of less than 3 ppt, whereas blooms of *Microcystis flos-aquae* occurred in salinity above 3 ppt. *Microcystis* blooms were most common and persistent in most of the alkaline, shallow, mostly mesotrophic to eutrophic lakes but rarely in oligotrophic lakes. Both species of *Microcystis* were often found together, although *M. flos-aquae* appeared to be dominant in late summer and autumn, when salinity levels were at maximum. Shape and size of colonies and cells were the stable morphological features differentiating the two species of *Microcystis*. Microcystins associated with these blooms ranged from < 0.5 to 1 645 µg L⁻¹ in wetlands and 0.05 to 124 µg L⁻¹ in the Swan River estuary. *Nodularia spumigena* blooms were confined to two freshwater lakes with salinity slightly below 3 ppt. This is the first time *N. spumigena* blooms are reported in freshwater lakes. The hepatotoxin nodularin was also detected in these wetlands, but at low levels.

Keywords: cyanobacterial blooms, urban lakes, Swan-Canning estuary, *Anabaena, Microcystis, Nodularia*, taxonomy, toxicity

Introduction

The wetlands of the Perth metropolitan area are characteristically shallow (mean depth < 2 m), alkaline with a mean electrical conductivity close to 900 µS cm⁻¹ (N = 80) and mostly mesotrophic, eutrophic or hypertrophic (Helleren 1993; John unpublished data 1998). They are surface expressions of superficial aquifers with their water levels under the influence of the water table and many receive substantial inputs from surface runoff. These wetlands experience a strong seasonal hydrologic cycle influenced by the Mediterranean-type climate with cool, wet winters and long hot, dry summers. Maximum water levels are observed from September to October, after the winter rains, and minimum levels in late autumn (March to April).

The Swan-Canning River estuary, the most prominent feature of the Perth metropolitan area, is a relatively shallow estuary with a strong seasonal flow of fresh and marine waters. Like most of the urban wetlands, the Swan River system itself has been experiencing harmful algal blooms in recent years. Minor blooms of *Microcystis* and *Anabaena* have occurred in the upper reaches of the Canning River (John 1987, 1994, 2000). Most of the surrounding wetlands in chains (east and west) located at both south and north of the estuary, are linked by

common geological and hydrologic features (Fig. 1) (Seddon 1972). Subsequent to the European settlement of Western Australia in 1829, intense agriculture, deforestation, urbanisation and damming of streams have gradually caused the deterioration of the estuary and the wetlands. Although there have been sporadic recordings of cyanobacterial bloom events (Atkins *et al.* 2001), and popular reference to toxic algal blooms, there has been very little published information on the distribution pattern of such blooms focussing on the taxonomy, seasonality, toxicity and environmental factors associated with these blooms. It is crucial to have accurate taxonomically defined spatial and temporal distribution records of harmful algal blooms for the management of these wetlands (Skulberg *et al.* 1993). The term 'blooms' is used in this paper to refer to dense growth of planktonic algae producing noticeable discolouration of water dominated by mostly one species (Graham & Wilcox 2000; Sze 1993). The number of cells in a bloom – mostly above 10 000 cells mL⁻¹ – varies according to the size of the cells and the dynamics of the bloom.

The objectives of the current project were to systematically study the ecology, taxonomy, seasonal (temporal) and geographic distribution and whenever feasible the toxicity of the cyanobacterial blooms. This paper presents an overview of the common cyanobacterial blooms in the Perth region, focussing on
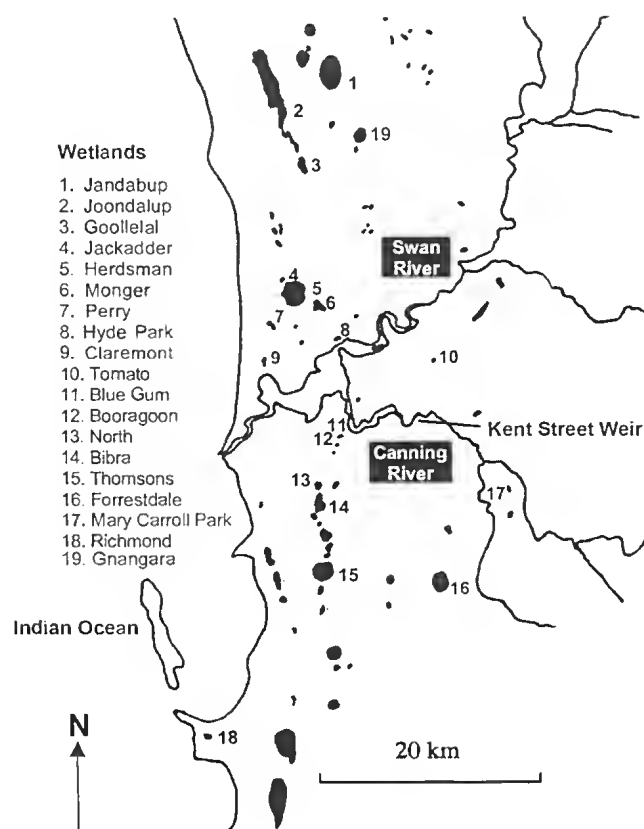
Figure 1. Map of the Swan Coastal Plain (Western Australia) showing the main wetlands and the Swan-Canning River estuary. The wetlands with *Microcystis* blooms recorded are indicated.

taxonomy and distribution, based on mostly unpublished data collected over the past 20 years.

Methods

Wetlands both south and north of the Swan River were investigated from 1985 to 2003. A total of 27 urban wetlands representing types both south and north of the river were seasonally surveyed for cyanobacterial blooms from 2000 to 2003. Toxic cyanobacterial blooms in the Canning River – the major tributary of the Swan River – were monitored from 1993 to 1994 and from 1996 to 2003. The environmental factors, taxonomy and dynamics of the first major toxic cyanobacterial bloom that resulted in the closure of the Swan River in February 2000 for several days were also studied. Integrated samples of phytoplankton representing the water column were collected at varying intervals (2 weeks to 3 months) mostly covering all the seasons, and water quality parameters (pH, Electrical Conductivity/salinity), nutrients (N and P), temperature, chlorophyll *a* and toxin concentrations in selected samples were determined according to standard methods (American Public Health Association 1975; Chorus & Bartram 1999; Chorus 2001). Water temperature, pH, electrical conductivity (EC) and salinity were measured using a portable TPS WP-81 meter in the field. Water samples from selected lakes were analysed for chlorophyll *a* and nutrients (inorganic and organic nitrogen and phosphorus) at the Chemistry

Centre (Perth) or SGS Environmental Services (Welshpool). One-litre concentrated algal samples were used for the detection of the relevant cyanotoxin by High Performance Liquid Chromatography by the Australian Water Quality Centre (Bolivar).

Integrated water samples were used for enumeration of cells and net samples (mesh size 25 µm) were used for concentrating algae, which were used for determination of toxins. The morphology of the colony and cells was measured and the species were identified using specialised literature (Geitler 1932; Desikachary 1959; John 2002; Komárek & Anagnostidis 1998, 2005; Baker 1991, 1992; Baker & Fabbro 2002; McGregor & Fabbro 2001).

Results

Microcystis aeruginosa Kützing (Fig. 2A) was present in almost all wetlands except the acidic Lake Gnangara (pH 3.5) irrespective of the nutrient status, but has occurred in bloom proportions (more than 20 000 cells mL^{-1}) during spring to autumn (September to April) in most of the alkaline mesotrophic to hypertrophic lakes. Over 85% of the urban lakes experienced *Microcystis* blooms. In hypertrophic lakes south of the Swan River (Bibra Lake, Thomsons Lake), *M. aeruginosa* blooms were persistent throughout the year and declined only during the mid-winter, with chlorophyll *a* values peaking to above 700 µg L^{-1} in 1993 (Fig. 3). Other wetlands in which *M. aeruginosa* blooms occurred are: Lake Richmond (1985, 1999), Herdsman Lake (1985, 2000–2003), North Lake (1990), Jandabup and Joondalup
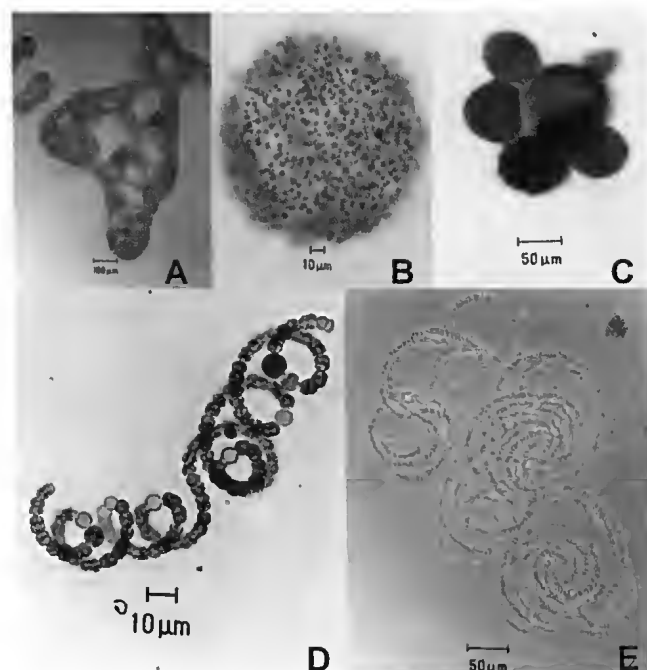
Figure 2. Cyanobacteria in wetlands and the Canning River in the Swan Coastal Plain. A, *Microcystis aeruginosa* Kützing (note the clathrate (gaps) nature of the colonies); B, a single colony of *Microcystis flos-aquae* (Wittrock) Kirchner; C, a cluster of colonies of *Microcystis flos-aquae* (note the compact nature of the colonies without gaps); D, *Anabaena spiroides* (Elenkin) Komárek; E, *Anabaena circinalis* Rabenhorst.
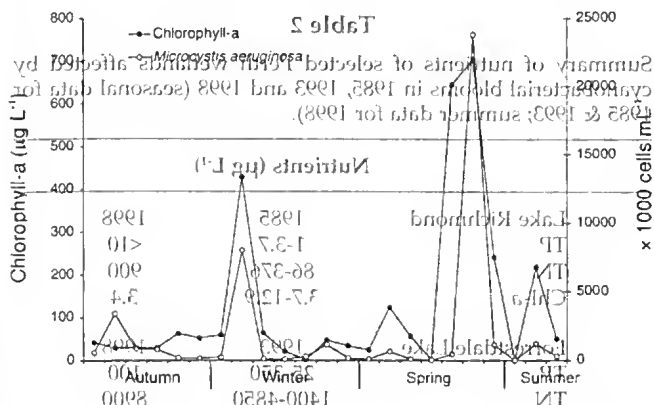
Figure 3. Seasonal distribution of *Microcystis aeruginosa* in Bibra Lake (a hypertrophic lake) in 1993 (integrated samples from 4 sites).

Figure 5. Distribution of *M. aeruginosa* and *M. flos-aquae* according to salinity of 14 wetlands (0.11–5.70 ppt) from 2000 to 2003, arranged in decreasing salinity.

(2003), Lake Goollelal (2000, 2001), Hyde Park (2000–2002), Lake Monger (1987), Perry, Blue Gum, Booragoon and Jackadder Lakes (2003) (Fig. 1).

The *Microcystis* blooms observed in Lake Richmond in 1985 and 1999 were mild and co-existed with unicellular green algae. Chlorophyll *a* levels from 3.7 to 12.9 µg L^{-1} and nutrient levels measured seasonally indicated it was an oligotrophic lake.

M. aeruginosa typically displayed spherical cells (diameter 4.8 to 15.3 µm), arranged in lobed clathrate colonies with distinct gaps/ of varying size, and were found in blooms in most of the wetlands and Canning River in the salinity range of 0.11 to 1.15 ppt. Mild blooms of *Microcystis flos-aquae* (Wittrock) Kirchner (Fig. 2B & C) coexisted with *M. aeruginosa* in most of the wetlands and caused a massive bloom in the Swan River estuary in February 2000, following a record rainfall of 102–206 mm in January with numbers up to 3 million cells mL^{-1}. The colonies were spherical without fenestrations (gaps) and the daughter colonies tended to bud-off with compactly arranged spherical cells (cell diameter 2.9 to 3.6 µm) (Fig. 4). Although *M. flos-aquae* coexisted with *M. aeruginosa* at lower salinity levels, the former dominated the wetlands only at higher salinity levels.

Figure 4. Mean diameter of cells of *Microcystis aeruginosa* and *M. flos-aquae* from 9 wetlands, 2000 to 2003, with standard deviation (N = 50 cells each taxa).

The species was found in a salinity range of 0.12 to 5.7 ppt (Fig. 5). Those sites dominated by *M. flos-aquae* also had *Anabaenopsis elenkinii* (Fig. 6A) – a cyanobacterium species with moderate salinity tolerance.

Temporally, both species of *Microcystis* caused blooms in spring to autumn; *M. flos-aquae* during the summer-autumn period when the salinity level increased to the maximum. Although *Microcystis* species were present in spring to autumn in almost all the wetlands and Canning River, they persisted in the hypertrophic lakes such as Lake Bibra, Hyde Park and Thomsons Lake, almost throughout the year.

Most dominant filamentous cyanobacterial blooms were caused by species of *Anabaena* (Nostocales). *Anabaena spiroides* (Elenkin) Komárek (Fig. 2D) and *A. circinalis* Rabenhorst (Fig. 2E) were observed in blooms from September to April in many of the wetlands (Herdsman Lake, Lake Joondalup, Lake Claremont, Tomato Lake, North Lake and Mary Carroll Park from 2000 to 2003) and the Canning River upstream of the Kent Street Weir from 1993 to 1994 and 1996 to 2003, close to the Canning River. These were short-lived. Apart from the hypertrophic wetlands, the most severe *Anabaena* blooms were in the upper Canning River from 1993 to 1994 following the removal of a massive *Hydrocotyl* infestation in 1993. Cell numbers up to 2 x 10^{6} cells mL^{-1} and chlorophyll *a* up to 820 µg L^{-1} were recorded in the autumns of 1994 and 1995. The nutrient levels in the upper Canning River in 1994 showed the highest concentrations were associated with *Anabaena* blooms (Table 1). Since then there have been such blooms in the Canning River almost every year. Warning signs against swimming have become a permanent feature derived from the close-by riverine wetlands or flushed from the Avon River.

The hepatotoxins, microcystin and nodularin, were microcystin concentrations in the Swan River in Herdsman 2000 ranged from 0.05 to 124.16 µg L^{-1}. In the wetlands from 1999 to 2000, microcystin concentrations of 0.5 to 1645 µg L^{-1} and nodularin concentrations from 0.5 to 2.1 µg L^{-1} were recorded (Kemp & John 2006). Nodularin was detected in Lake south of Australia, the neurotoxin, was not detected in the blooms of *Anabaena*.

Discussion

1985 cyanobacterial blooms in blooms in wetlands are good indicators of degraded community Systems (Paerl 1988). Algal status they... freshwater taxa can be determined by Anabaena (Hillebrand & Paerl 1988). The type of algal blooms associated with mesotrophic and eutrophic conditions are well recorded in the literature (Wetzel 1983). The data collected over the past 20 years on cyanobacterial blooms as shown above reflect the mesotrophic to eutrophic status of most Perth wetlands. Many of the freshwater species are able to synthesise toxins (cyanotoxins) that affect the liver (microcystins and nodularins) or nervous systems (saxitoxin), making such blooms a health hazard. Although no anatoxins have been reported from *Anabaena* blooms in Australia (Bell'an & Neilan 2000), mouse assay tests have been confirmed to be positive for many of the blooms e.g., *Anabaena* blooms in the Canning River (Hosja & Deeley 1994).

The minor species, those that have not yet caused severe blooms may present a future threat (Falconer 1993) in Australia, *Cylindrospermopsis raciborskii* blooms are more common in the eastern states, especially in drinking water sources in subtropical and tropical Queensland (McGregor & Fabbro 2000). In temperate Australia, it has been reported only from Perth wetlands, when water flushed during summer months when water temperatures are high.

Table 1

Nutrients (µg L^{-1}) and nutrient ratios in the Canning River from February to December 1994, covering seasonal variation.

Nutrients	Surface		Bottom	
	Min	Max	Min	Max
TP	30	710	30	11000
FRP	10	170	10	8100
TN	230	9600	840	80
Anoxia	10	2000	10	13
TN:TP	0.25	53	0.10	0.10
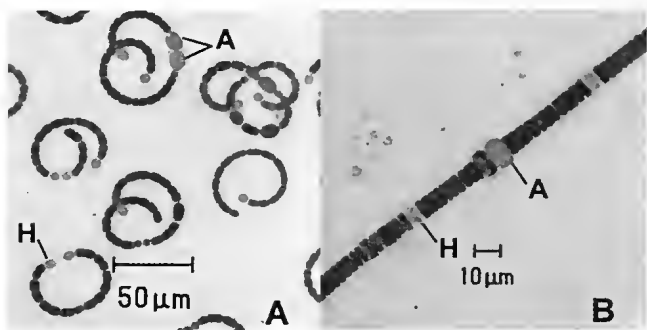
Figure 6. A, *Anabaenopsis elenkinii* (note the position and size of the akinetes (A) and heterocysts (H)); B, *Nodularia spumigena* (note the akinetes and heterocysts).

the upper Canning River due to the toxic *Anabaena* blooms.

Anabaena spiroides was often seen to coexist with *A. circinalis*. The shape of the akinete (broadly ovate in the former and oblong ovate in the latter) appears to be a more reliable character to separate the two, rather than the nature of the spiral, which can vary a lot in the latter.

Other *Nostocales* species observed in the wetlands in minor blooms were *Anabaena flos-aquae* (Lyngbye) de Brébisson et ex et Flahault, *Anabaena oscillarioides* Bory, *Anabaenopsis arnoldii* Aptekarj (Lake Claremont, 2001), *Anabaena bergii* var. *limnetica* Ostenfeld (Mary Carroll Park, 2003), *Anabaenopsis elenkinii* Miller (Lake Joondalup, Bibra Lake, 2003), *Aphanizomenon gracile* Lemmermann (Bibra Lake, 2000), *A. ovalisporum* (Bibra Lake, Emu Lake, 2002) and *Cylindrospermopsis raciborskii* (Bibra Lake, 2001). In addition to Mary Carroll Park, this species has also been observed in Lake Joondalup, Lake Brearely, Lake Coogee and Emu Lake.

Nodularia spumigena Mertens blooms (Fig. 6B) were first recorded in 1993 in two southern freshwater wetlands (Forrestdale Lake and Thomsons Lake), located close to the Canning River. These were short-lived blooms and lasted for 4 weeks. Since then, every spring-summer these blooms have been observed. Before and after the *Nodularia* blooms, *M. flos-aquae* blooms were commonly observed in these wetlands. Salinity close to 3 ppt was associated with *Nodularia* blooms. Both lakes are shallow, often less than 1 m deep, and dry up during severe summers.

Nodularia spumigena was also observed in low numbers along with the bloom of *Microcystis flos-aquae* in the Swan River estuary in February 2000, most likely derived from the close-by riverine wetlands or flushed from the Avon River.

The hepatotoxins, microcystin and nodularin, were associated with the selected blooms analysed. Microcystin concentrations in the Swan River in February 2000 ranged from 0.05 to 124.16 µg L^{-1}. In the wetlands from 1999 to 2000, microcystin concentrations of 0.5 to 1645 µg L^{-1} and nodularin concentrations from 0.5 to 2.11 µg L^{-1} were recorded (Kemp & John 2006). Nodularin was detected in two southern lakes in association with a *Nodularia spumigena* bloom. As with the rest of Australia, the neurotoxin, anatoxin, was not yet detected in the blooms of *Anabaena*.

Table 2

Summary of nutrients of selected Perth wetlands affected by cyanobacterial blooms in 1985, 1993 and 1998 (seasonal data for 1985 & 1993; summer data for 1998).

Nutrients (µg L^{-1})		
Lake Richmond	1985	1998
TP	1-3.7	<10
TN	86-376	900
Chl-*a*	3.7-12.9	3.4
Forrestdale Lake	1993	1998
TP	25-350	100
TN	1400-4850	8900
Chl-*a*	0.4-61.8	3
Bibra Lake	1993	1998
TP	30-260	20
TN	1200-9000	1400
Chl-*a*	1.6-702.9	18
Thomsons Lake		1998
TP		170
TN		3100
Chl-*a*		20

High pH (7.5–9), high temperature (24–28 °C), chlorophyll *a* values from 7 to 700 µg L^{-1} and eutrophic conditions were associated with most of the recorded blooms. Lake Richmond was an exception: nutrient concentrations pointed to an oligotrophic status, although mild blooms were persistent in 1985. A summary of water chemistry of selected wetlands is presented in Table 2.

Discussion

Nuisance cyanobacterial blooms in freshwater wetlands are generally indicative of degraded eutrophic systems (Boulton & Brock 1999). Trophic status (trophy) of freshwater lakes can be determined by chlorophyll *a*, TP and TN according to OECD boundary values (Ryding & Rast 1989). The type of algal blooms associated with mesotrophic and eutrophic conditions are well recorded in the literature (Wetzel 1983). The data collected over the past 20 years on cyanobacterial blooms as shown above reflect the mesotrophic to eutrophic status of most Perth wetlands. Many of the freshwater species are able to synthesise toxins (cyanotoxins) that affect the liver (microcystins and nodularins) or nervous system (saxitoxin), making such blooms a health hazard. Although no anatoxins have been reported from *Anabaena* blooms in Australia (Beltran & Neilan 2000), mouse assay tests have been confirmed to be positive in many of the blooms e.g. *Anabaena* blooms in the Canning River (Hosja & Deeley 1994).

The minor species, those that have not yet caused severe blooms, may present a future threat (Falconer 1993). In Australia, *Cylindrospermopsis raciborskii* blooms are more common in the eastern states, especially in drinking water sources in subtropical and tropical Queensland (McGregor & Fabbro 2000). In temperate Australia, blooms have been restricted to the summer months when water temperatures reach the

mid twenties (Bowling 1994; Hawkins *et al.* 1997). *Cylindrospermopsis raciborskii* was detected in Bibra Lake during autumn to late winter when water temperatures were generally less than 17 °C. This species is a threat due to its invasive potential and reports of both animal and human poisonings due to cylindrospermopsin, a distinct alkaloid hepatotoxin present in this species. Cylindrospermopsin production has also been demonstrated in Australian strains of *A. bergii* var. *limnetica* (Schembri *et al.* 2001). *Aphanizomenon ovalisporum* is a relatively new species identified in Australian waters and is also capable of producing cylindrospermopsin (Shaw *et al.* 1999). The toxins produced by these two species are a major health concern in the eastern states (Jones 2003).

The shallow, alkaline wetlands in the Swan Coastal Plain are 'designed' for cyanobacterial blooms with the sandy soil permitting easy leaching of phosphorus and nitrogen from a catchment depleted of native vegetation and subjected to urbanisation and intense farming. Prolonged periods of high temperature (spring to autumn) and winter rains discharging nutrients into the wetlands have provided the most conducive conditions for autochthonous cyanobacterial blooms. The high EC of the wetlands tends to favour salt tolerant species like *Nodularia spumigena* and *Microcystis flos-aquae*, the latter forming widespread opportunistic allochthonous blooms even in the most unlikely environments such as the Swan River estuary. The link between Perth wetlands and the Swan River estuary was well established by the unusual high rainfall in summer-autumn of 2000 followed by the above bloom. Microcystin concentrations of cyanobacterial blooms in the southwest of Western Australia have been recently reviewed by Kemp & John (2006). The Swan River estuary is vulnerable to most of the freshwater cyanobacterial blooms discussed in this paper, if alterations in nutrients and salinity occur. The urban wetlands have not received adequate attention as a source of cyanotoxins hazardous to human health. Regular monitoring for toxins is required.

The upper reaches of the Canning River, since the establishment of the Kent Street Weir with its annually adjusted height, and Canning Dam, have been transformed into an impoundment of eutrophic freshwater 'wetland' – somewhat similar to the shallow hypertrophic southern wetlands close-by. Prolonged *Anabaena* blooms in the Canning River point to the similarity in water quality between the river and nearby wetlands. Increasing salinity during spring-summer in the southern wetlands provides ideal conditions for *Nodularia* blooms to occur and they are likely to become widely distributed as the wetlands become more eutrophic and saline.

Nodularia spumigena blooms are often associated with saline wetlands and estuaries. The Peel-Harvey system had experienced severe blooms of *N. spumigena* in a salinity range from 3 to 30 ppt (Lukatelich & McComb 1986; McComb & Lukatelich 1995) since the late 1970s to 1993 when the Dawesville Channel was built.

This is the first time *Nodularia* blooms have been recorded in such low salinity waters in Australia. *Nodularia* blooms have been reported from saline waterbodies from other parts of Australia (Jones 2003) and not from freshwater bodies. The fact that short-lived

Nodularia blooms were observed in two Perth freshwater wetlands whose salinity levels rose to 3 ppt before the blooms, should be a matter of great concern. The recurrence of such blooms for prolonged periods in the future is very likely, as salinity and phosphorus levels increase in the wetlands.

Conclusions

1. *Microcystis aeruginosa* and *M. flos-aquae* are the most ubiquitous bloom-forming cyanobacteria in the Perth region. Both *M. aeruginosa* and *M. flos-aquae* coexist in most of the wetlands with peaks in spring to autumn but the latter forms blooms in lakes of higher salinity (above 3 ppt).

2. The upper Canning River in summer becomes a eutrophic freshwater impoundment resembling the shallow wetlands nearby and *Anabaena* and *Microcystis* blooms have been common in the Canning River since 1993.

3. *Nodularia* blooms are confined to the hypertrophic southern wetlands with salinity close to 3 ppt and are short lived. As salinity increases in the eutrophic wetlands, there is the likelihood of more prolonged *Nodularia* blooms.

4. Many of the minor toxic blooms of *Anabaenopsis*, *Aphanizomenon* and *Cylindrospermopsis* are likely to increase as eutrophication increases.

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Ancient weathering zones, pedocretes and palaeosols on the Australian Precambrian shield and in adjoining sedimentary basins: a review

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Abstract

A stratigraphic approach is used in this review of ancient weathering zones, mottled zones, pedocretes and palaeosols on the Australian Precambrian Shield and in adjoining sedimentary basins. Pedogenic features identified in the landscape during regional stratigraphic mapping have been traced along the western margin of the Australian Precambrian Shield. The weathered zones, pedocretes, mottled zones and palaeosols identified in South Australia and elsewhere have been extended into the Perth Basin where there are correlative conformities. The weathered zones, pedocretes, mottled zones and palaeosol units are described in a geochronological framework from Palaeozoic to Late Cainozoic. The weathering products of the Palaeozoic include the Playfair Weathering Zone. Mesozoic sequences include the Arckaringa Weathering Zone (a pallid zone in laterite profiles) and the San Marino mottled zone equivalent. The units taken together have been said by some authors to form "a distinctive basal horizon which underlies all true laterites". The laterite in this sense refers to the ferricrete forming a caprock on older materials. Early and Middle Cainozoic sequences include bauxite, the Greenmount Ferricrete and the Calingiri Silcrete. Late Cainozoic sequences contain the Jumperdine Ferricrete and the Karoonda Soil (which in some places is a syndepositional silcrete), and the mottled zones of lateritic podzolic soils. The weathered zones, pedocretes and palaeosols were formed under different climatic regimes. The study of weathering zones, pedocretes and palaeosols on the south-west margin of the Australian Precambrian Shield confirms the earlier conclusions derived from South Australia that sedimentary sequences are intercalated in the profiles between the Playfair Weathering Zone and the Arckaringa Weathering Zone, between the San Marino mottled zone equivalent and the Greenmount Ferricrete, and (after erosion of the ferricrete and formation of the Calingiri Silcrete) between the Playfair Weathering Zone and the younger Jumperdine Ferricrete. Sediments also are intercalated between the Jumperdine Ferricrete and the Karoonda Palaeosol.

The major implication of the work is that pedogenic features can be correlated Australia-wide on a morphological basis and according to their time of origin.

Keywords: weathering zones, pedocretes, palaeosols, stratigraphy, Western Australia, South Australia.

Introduction

The aim of this review is to place weathered zones, pedocretes and palaeosols on and around the Australian Precambrian shield in a stratigraphic setting, synthesising the information mainly from Western Australia and South Australia, but relating them to other sections in the eastern states where appropriate. Older pedogenic features are well preserved on the Precambrian shields, but they are down-faulted and buried by sediments in the marginal basins.

The location of weathering zones, pedocretes and palaeosols has been established on 1:250,000 geological maps compiled by the Geological Surveys of Western Australia, South Australia and the Bureau of Mineral Resources. The youngest substrate on which the material has been developed and the oldest unaltered rock or soil unit overlying it are identified. This procedure places the weathering zone, pedocrete or palaeosol in a stratigraphic position relative to other materials at the formation or stage level in the geological column for that area.

Each of the weathering zones, pedocretes or palaeosols serves to identify a bounding surface in sequence stratigraphy (Salvador 1994; Embry *in* Brakel 2003). These surfaces can be placed in the record of adjoining sedimentary basins according to their time of formation, a procedure that identifies sequences larger than a group or supergroup throughout the study area. The relevant basin stratigraphy has been described in the Perth area by Cockbain (1990) and Trendall & Cockbain (1990), and on the south-east margin of the shield by Firman (1975, 1980) and Drexel *et al.* (1993). The comments on basin sediments herein are summarized from these texts except where other references are given.

Although the ancient weathering zones, pedocretes and palaeosols could be as old as the sedimentary unit in or on which they have been developed, other evidence has been taken into account when suggesting the time of formation. In many cases, the age of the rock units with which they are stratigraphically associated is shown in the records of sedimentary basins and has been previously determined by palaeontological criteria (Cockbain 1990; Ludbrook *in* Drexel & Preiss 1995).

The pedogenic features described on the western margin of the shield have been matched to similar

features on the south-east margin of the shield where they have been described and named (Firman 1994). The major implication of this work is that pedogenic features can be correlated Australia-wide on a morphological basis and according to their time of origin.

There are problems, however, with definitions of weathering zones, pedocretes and palaeosols, and for this reason some notes are provided here to clarify their use in this paper.

Soil consists of layers (horizons) developed below ground surface by soil forming processes operating in different ways at different times. All the layers, other than those relating to the modern environment are old. Assemblages of layers constitute soil profiles in the pedological sense (Firman 1969b, 1971).

Horizons of accumulation (B horizons) characterize particular profiles at the great soil group level. On the soil stratigraphic table (Fig. 1), surface soils are indicated by their B horizons and by the great soil groups with which they are associated. The soils overlie pedocretes and weathering zones commonly occurring in the Adelaide Region of South Australia. Similar soils in the Perth Region of Western Australia are described by McArthur & Bettenay (1960) and other soil scientists mentioned in this text.

Where a break in soil formation is followed by emplacement of younger material (either sediment or soil), a palaeosol may be recognized. Some soil profiles in the pedological sense are storied profiles and may include a number of palaeosols (Firman 1979, 1986; Yaalon 1971). The distribution of these soils has been outlined on maps of South Australia (e.g., Firman 1986), and their evolution has been described in Firman (1988, 1994).

The term pedocrete is used to describe superficial materials that were originally weathering residues or sedimentary layers in soil profiles. These materials have undergone cementation by minerals precipitated from groundwater (cf. Netterburg 1985).

Ironstone is an old term for ferricrete that indicates the cementing agent and the use of the metal as an ore. Ferricrete is commonly called laterite in early Australian literature, but the term is a misnomer derived from a supposed equivalence with clay used for brick-making in India. Ferricretes and silcretes have been called caprocks to emphasize their position in the landscape, and duricrusts to identify their hardness. Ferricretes and silcretes form the upper part of giant profiles overlying ancient weathering zones. These profiles are described as laterite and silcrete profiles in the Australian literature.

Where the parent material below a soil stratigraphic unit in Western Australia differs from that in a profile or section in South Australia another name is used. Although individual soils and pedocretes are stratigraphically associated with weathered rocks and surficial sediments in particular provinces or sedimentary basins where they were first described, they can be traced for great distances through different landscapes, into adjoining sedimentary basins, along the piedmont zones of mountain chains, river cliffs, and coastal margins.

The Australian Precambrian Shield

The Australian Precambrian Shield includes the Yilgarn Craton and the Pilbara Craton in the west and the Gawler Craton and Musgrave Block in the south-east. Proterozoic rocks which are shown north-east of the cratons (Figs 1, 2 & 3) are bounded by younger Phanerozoic rocks.

Much of the detailed evidence on ancient soils along the south-west margin of the Australian Precambrian Shield is derived from a narrow bench, described as a "laterite platform" and named the Ridge Hill Shelf by Woolnough (1918). The evolution of the shelf provides evidence important in the understanding of the regional stratigraphy of Phanerozoic sedimentary deposits and of associated weathering zones, pedocretes and palaeosols. The shelf, which is about 135 m below the top of the Darling Scarp and 80 m above sea level, is from one and a half to three kilometres wide and extends from Eneabba in the north to near Tutunup in the south – approximately a distance of 500 kilometres (Fig. 2). The shelf diverges from the Darling Scarp to the north and south to follow the western margin of Mesozoic sequences which on their eastern side are at much the same elevation as the shield itself.

The shield margin in the west is a fault zone across which the ancient shield rocks have been displaced over 15 km in the central Dandaragan Trough. The fault zone, which was named the Darling Fault (Saint-Smith *in* Jutson, 1934) is a N-S geofracture some 500 km in length, which separates Archaean and Proterozoic rocks of the Australian Precambrian Shield to the east of the fault – here represented by the Yilgarn Craton – from Phanerozoic sediments and volcanics of the Perth Basin to the west – here represented by the Dandaragan Trough and the Bunbury Trough which adjoins to the south.

Archaean rocks are part of the Yilgarn Craton, a stable nucleus composed of granites and gneiss enclosing a number of "greenstone belts" of metamorphosed layered
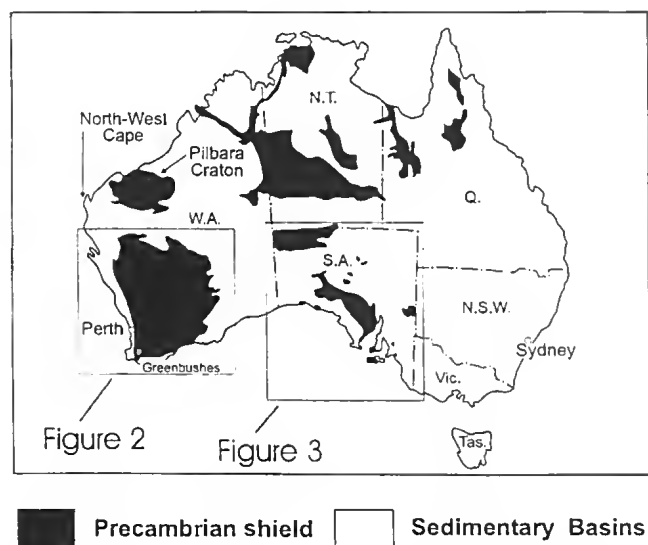
Figure 1. Map showing the Precambrian Shield, and insets of the Study Areas in Southwestern Australia and in South Australia.
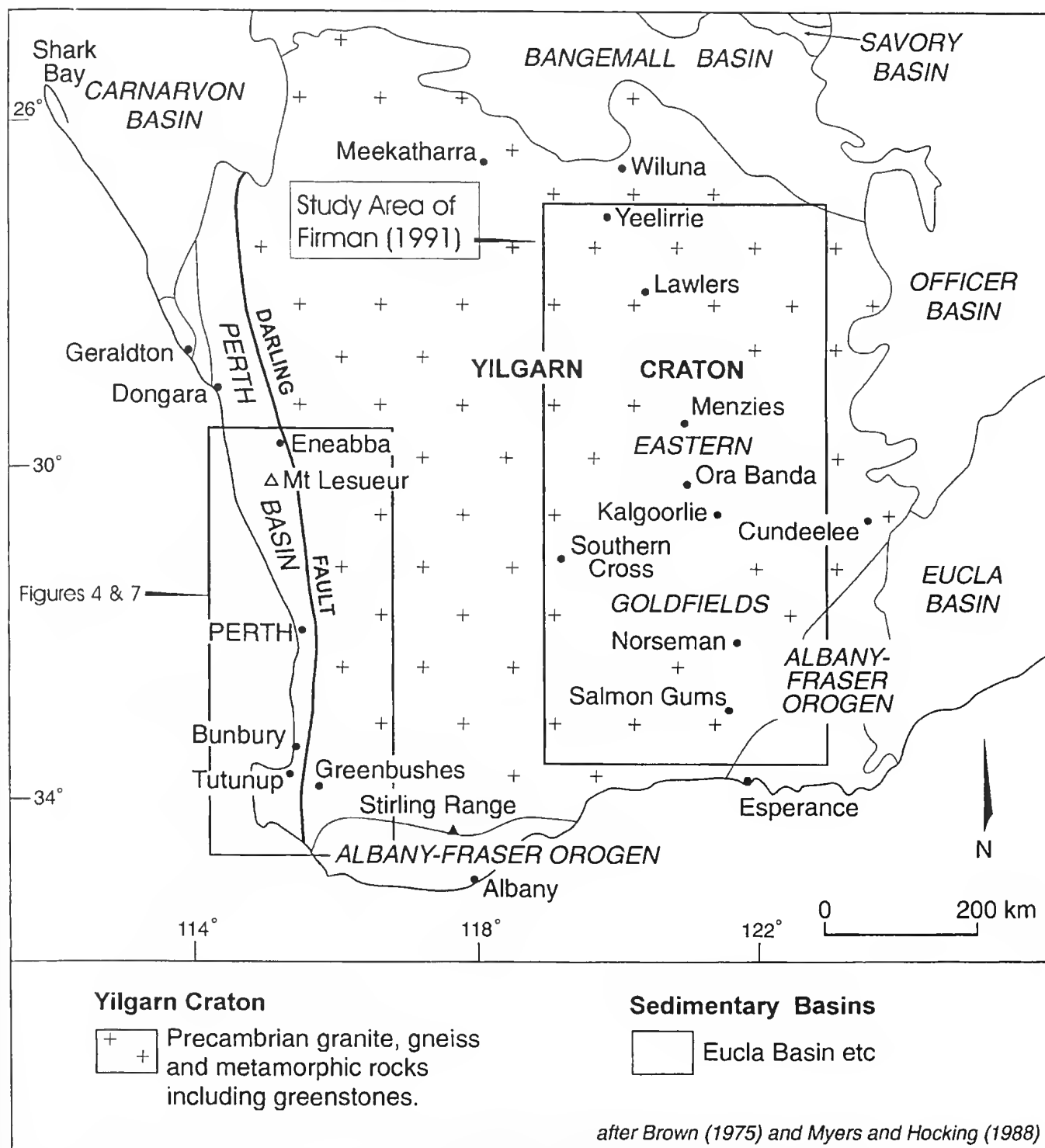
Figure 2. Location of the south-west margin of the Australian Precambrian Shield, the Yilgarn Craton, Pilbara Craton and adjoining sedimentary basins. The figure indicates the area along the Darling Fault where palaeosols, pedocretes, mottled zones and weathering zones are extended into parts of the Perth Basin where there are correlative conformities. The boxed area centred over Kalgoorlie is the study area presented in Firman (1991).

rock. The basement rocks on the western margin of the shield are part of the Western Gneiss Terrain, the most western unit defined within the Yilgarn Craton by Myers 1990 (see Granitic Rocks in Fig. 4).

Proterozoic rocks are Middle Proterozoic according to Myers & Hocking (1988). They were part of the extensive cover of sedimentary rocks containing stromatolites and trace fossils, which are now exposed over a wide area in northern Australia, and in erosional remnants of rocks containing an Ediacran fauna in the Stirling Range in the south and the Ediacra Range in South Australia.

Tholeiitic quartz dolerite dykes intrude all the Precambrian rock-types including the Proterozoic. Giddings (1976) reports six episodes of dyke intrusion, ranging from the Archaean to Late Precambrian. The dykes which cut the Cardup Group (Cardup Series of Prider 1943), are presumed to be Late Proterozoic or younger. They are the youngest crystalline basement
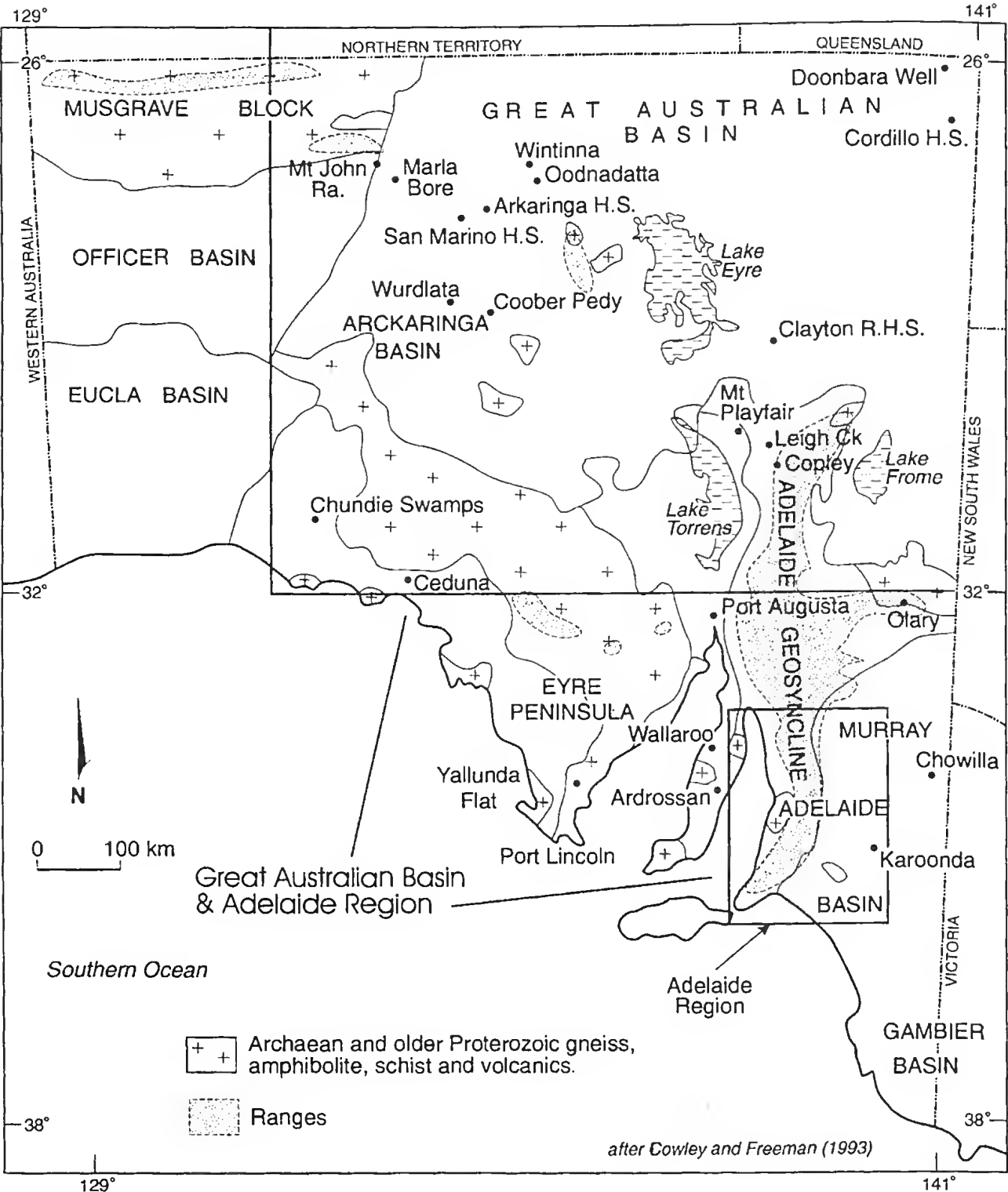
Figure 3. Important localities on the south-east margin of the Australian shield in South Australia. The boxes show areas where studies of soil – geology have been made and palaeosols, pedocretes, mottled zones and weathering zones have been mapped at 1:250,000 scale. For details of the Adelaide Region see Firman (1986, 1988). For details of the Great Australian Basin area see Firman (1980).
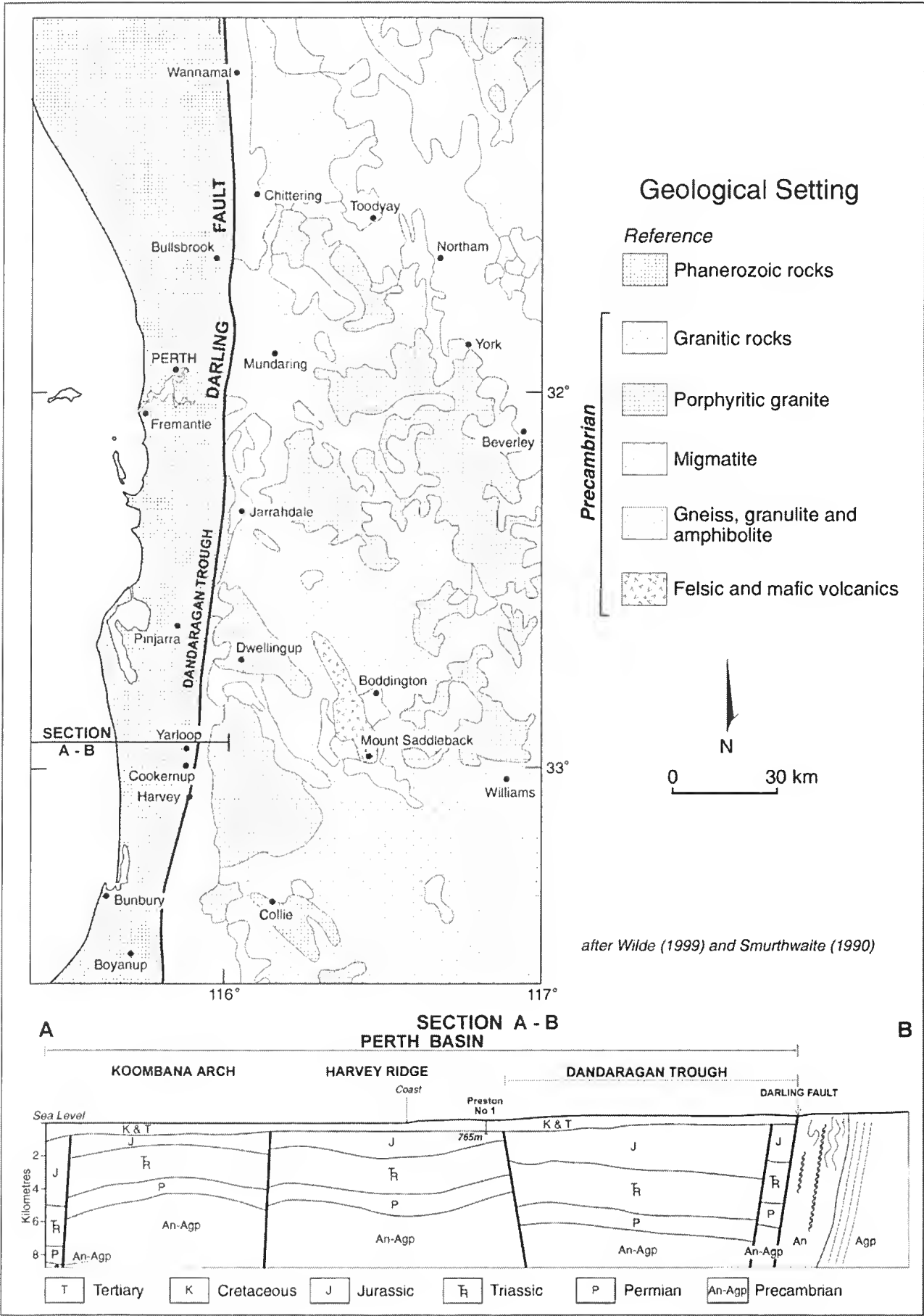
Figure 4. The geological setting of the south-west margin of the shield. Precambrian rocks east of the Darling Fault Zone and Phanerozoic sediments of the Perth basin to the west. Map supplied by Professor Simon Wilde.

rocks on the margin of the shield affected by the oldest weathering zone at the base of laterite profiles.

The Precambrian on the south-east margin of the shield is described in relation to morpholithological features relevant to this study by Firman (1975) and in more detail by Drexel *et al.* (1993).

Palaeozoic – sedimentation and weathering

The geological history of the Australian Precambrian Shield subsequent to its early development is recorded in important stratigraphic sequences on the margins of the shield where they are exposed by exoreic drainage. Within these sequences, stratigraphically associated or

SOIL STRATIGRAPHIC TABLE

Palaeosols, Pedocretes and weathering zones	Age	Great soil groups	Lateritic podzolic	Solodic	Red-brown earth	Solonized brown soil	Black earth, terra rossa and rendzina[d]	Red and yellow podzolic	Solonchack	Siliceous and calcareous sand	Skeletal soil
Sandy A horizons etc.			+	+	+	+	+	+	+	+	+
Alluvial and estuarine soils									+		
Peebinga Soil	1					+					
Loveday Soil						+		+			
Callabonna Soil	2				+		+	+			
"Wilkatana" soil					+						
Bakara Soil	3				+		+				
Ripon Calcrete					+						
Ardrossan Soil	4				+						
Older structured clays				+	+						
Denison gypcrete											
Karoonda Soil	5		+								
Jumperdine Ferricrete[a]	6		+								
Calingiri Silcrete[b]	7		+								
Greenmount Ferricrete[c]	8		+								
San Marino mottled zone	9		+								
Arkaringa Weathering Zone	10		+								
Playfair Weathering Zone	11		+								

S.A. examples
a. Ferricrete on Loxton Sand
b. Clayton River Silcrete
c. Yallunda Ferricrete
d. Black earths and red-brown earths

Figure 5. The diagram shows the relative stratigraphic position (youngest at the top to oldest at the bottom) of palaeosols, pedocretes, mottled zones and weathering zones found in surface soils and substrates in an around the Australian Precambrian Shield. The crosses record the presence of master horizons in soils at the great soil group level and of pedocretes, mottled zones and weathering zones encountered in this study. Note that some soils are multi-storied. The numbers in the age column indicate geological time as follows: 1. Recent; 2. Late Pleistocene; 3. Medial Pleistocene; 4. Pliocene- Pleistocene; 5. 2.5 m years +; 6. Pliocene; 7. Miocene; 8. Eocene- Miocene; 9. Late Cretaceous - early Eocene; 10. Late Cretaceous; 11. Palaeozoic. Numbers 1– 4 are from Firman, 1988. Numbers 5 – 11 are from the present text and are supported by palaeontological studies quoted herein and by palaeomagnetic dating (Idnurm & Senior, 1978). Lower horizons and weathered substrates are omitted from the table.

as companion materials, weathering zones, pedocretes and palaeosols were developed which individually and as assemblages of layers and horizons record the history of weathering and of soil formation since the Proterozoic. Soil stratigraphic units, and their stratigraphic context are shown in Figures 5 & 6). On the south-west margin of the shield, the geological record east of the Darling Fault can be interpreted in part from Proterozoic rocks preserved in scattered outcrops at a high level along the Darling Scarp, and Permian, Mesozoic and Cainozoic rocks exposed by the erosion of fault blocks or preserved in grabens, deep embayments and ancient valleys (Playford *et al.* 1975; Hocking & Cockbain 1990).

STRATIGRAPHIC TABLE

		Perth Basin	Darling Range & Eastern Goldfields	S. E. Shield Margin
Pleistocene *		Mottling Guildford[1] Formation	Valley Fill Menzies Fm.[1]	Ardrossan Soil Blanchetown Clay[1]
Pliocene	*	Karoonda Soil		
		Guildford Fm[3]		Blanchetown Clay[2]
		Yoganup Fm.	Sands and gravels	Avondale Clay
				Parilla Sand etc
	*	Jumperdine Ferricrete	Ferricrete[2]	Ferricrete[3]
		Ascot Formation	Sandy valley fill	Loxton Sand
Oligocene-Miocene*		Stark Bay Fm		Etadunna Formation[4]
			Calingiri Silcrete	Clayton River Silcrete
			Fluvial sediments[3]	Waste mantle
Eocene-Miocene *		Greenmount[4]	Ferricrete	Yallunda Ferricrete
Paleocene-Eocene		Kings Park Fm.	Darling Range Bauxite	Pidinga Formation[5]
Mesozoic	*	San Marino mottled zone.[5]	San Marino mottled zone	
	*	Arckaringa Weathering Zone		
		Sandstone[6]	Ridge Hill Sandstone	Winton Formation
				Bulldog Shale
Palaeozoic	*	Permian sediments		
		Playfair Weathering Zone		
				Cambrian and Ordovician sediments
Precambrian		Basement Rocks		Basement Rocks
* Weathering zones, pedocretes and palaeosols		1. Upper beds 2. Lateritic Podzols 3. Lower beds 4. Plateaux (Mooliabeenie, etc) 5. Poison Hill 6. Coolyena Grp	I. Yeelirie (lower beds) 2. Mulline Fm.	I. and Hindmarsh Clay 2. Lower beds 3. "Gun Emplacement" 4. also Nullarbor Ls. 5. Eyre Formation Inland

Figure 6. The stratigraphic table shows sedimentary units that bracket the weathering zones and pedogenic units in different profiles. Note the alignment of duricrusts and the alternation of iron and silica deposition. For the south-east margin of the shield, the names of sedimentary units down to Pidinga Formation relate to southern basins. Many of the names of units listed below the Clayton River Silcrete – with the exception of the Yallunda Ferricrete and Pindinga Formation – are found in or on the margin of the Great Australian Basin.
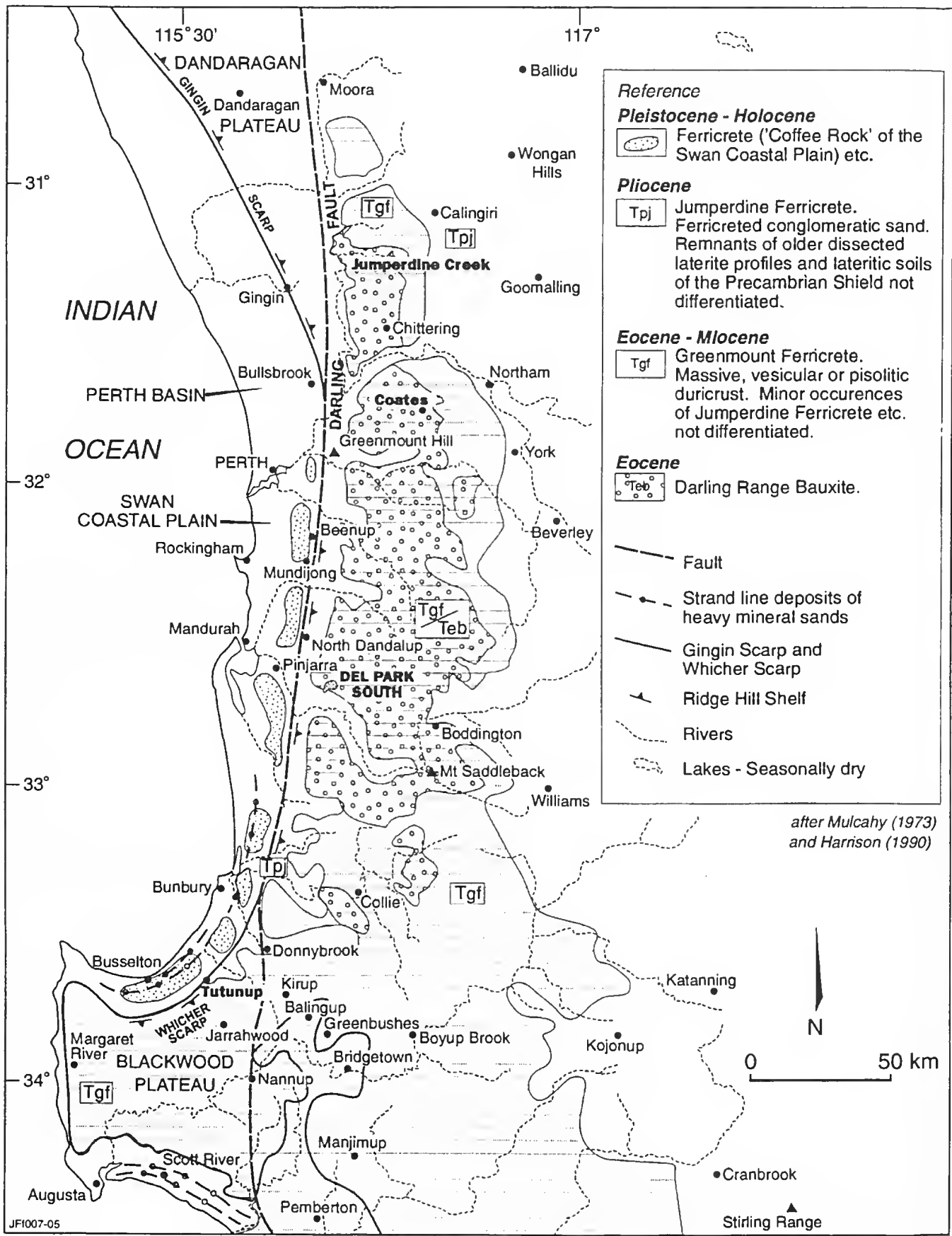
Figure 7. Geological map showing the distribution of ferricrete and bauxite on the western margin of the Precambrian Shield. Note that Greenmount Ferricrete also occurs to a limited extent on the Dandaragan Plateau, in the Gingin area near Poison Hill and at Mooliabeenie.

The Playfair Weathering Zone

In Western Australia, a polygenetic Palaeozoic erosion surface is postulated by Fairbridge & Finkl (1978). They state that the primordial surface on which the Playfair Weathering Zone was later developed may be traced back to post-Archaean/Early Proterozoic peneplantation visible in unconformities in the Stirling Range south-east of the study area.

The Playfair Weathering Zone is exposed in deep open pits in the Eastern Goldfields (Fig. 2), notably at the Agnew gravel quarry, and the Black Flag, Kanowna Belle and Panglo gold mines. In the Lawlers district of the Eastern Goldfields (Fig. 2) at the Genesis gold mine a Permian fluvioglacial palaeochannel is incised into the top of the Playfair Weathering Zone (Anand 1993a, 1993b). Along the western edge of the shield the zone is exposed by excavation of dams – the Serpentine Dam is a good example – and on the valley walls of streams incised through the Darling Scarp near Perth (Figs 2, 7 & 8).

Important sequences have been described near Yeelirrie in the Eastern Goldfields (Fig. 2), by Glassford (1987). The oldest named unit, Westonia Formation, is easily confused with *in situ* weathered Precambrian basement rock (Glassford 1987; de Broekert 2003). The presence of the formation between weathered basement and overlying "sandy lateritic to bauxitic duricrust" of uncertain age is incompatible with the notion of a direct genetic correlation between the weathered basement and the duricrust, the ferricrete of this study.

The Playfair Weathering Zone is named after Mount Playfair north-west of the type section, which is 2 km SSE of Copley in South Australia (Fig. 3). The unit is subhorizontal and has been developed on folded rocks of Precambrian, Cambrian and Ordovician age in the Mount Lofty and other ranges in South Australia, and on rocks of the Precambrian Shield on the margins of late Palaeozoic and Mesozoic basins elsewhere. It is characterized by large irregular red, yellow and white patches up to 10 m across. Thickness varies, but zones 100 m thick are common. The reader is referred to Firman (1994), and to the earlier work quoted therein showing important sections.

Near Adelaide, the palaeosurface on which the Playfair Weathering Zone was developed post-dates the folding of Proterozoic, Cambrian and Ordovician rocks along the Adelaide Geosyncline in the Delamerian Orogeny. In the north of South Australia, a similar weathering zone was developed near Marla, west of Oodnadatta (Fig. 3) possibly as early as the exposed erosional surface on the Cambrian Trainor Hill Sandstone (Firman 1980; Gravestock *et al.* 1995). Covering sediments are not present and the age of the weathering may be younger.

In the type section south of Leigh Creek (Fig. 3) 2 km south-east of Copley in South Australia (Firman 1980), the zone is overlain by Jurassic sediments. At Leigh Creek, coal measures of Middle Jurassic to Triassic age overlie the zone. Triassic and Permian sediments in adjoining basins are weathered, but do not show the thick, deeply weathered Playfair Weathering Zone. Another section, which is a possible supplementary section, occurs at Warramboo (Heath 1962) .

A similar weathering zone has been noted on early Palaeozoic rocks in New South Wales by the writer and in Victoria by Dr W V Preiss (per comm, 2002). A post-Ordovician/pre-Permian age is suggested for the Playfair Weathering Zone.

Younger Palaeozoic sequences

Much of the younger geological record is missing from the terrain east of the Darling Fault. A Silurian sequence is identified in the northern part of the Perth Basin. It includes quartz sandstone, carbonate rocks and evaporates (including tidal red beds). A Devonian – Carboniferous sequence is identified from reworked microfloras in Cretaceous and Permian rocks (Mory & Iasky 1996). A Late Carboniferous and Permian sequence was deposited by intermittent transgressions of a sea from the north. Continental sedimentation extended onto the Yilgarn Craton and coal-bearing sediments were deposited in the Collie, Wilga and Boyup basins. The lowest part of the Permian sequence is glacigene. In the north the Irwin Coal Measures and the Wagina Sandstone contain a well-developed Glossopteris fauna. There was a short-lived marine transgression in the Perth Basin during the Late Permian followed by uplift and erosion.

Mesozoic – sedimentation, weathering and development of the San Marino mottled zone

Weathering events during the Mesozoic on the Australian Precambrian Shield are not separately recorded in the literature, but the sedimentary record itself provides an indication of weathering and erosion in the provenance areas.

A Triassic sequence up to 3000 m thick is identified when the Perth Basin was again a rift valley which opened to the sea in the north. The base of the sequence is marked by a widespread unconformity. The main rock unit laid down as a result of tectonism, the Lesueur Sandstone, was probably deposited in a series of fans along the fault scarp. A Jurassic and Early Cretaceous sequence, which records the post-Gondwana phase of continental break-up, began when Australia and the rest of Gondwana separated and plate-margin settings became important.

The Bunbury Basalt, a vesicular porphyritic basalt, occurs near the base of the sequence. The basalt erupted at 123 and 130 m.y. (Wilde 1999). During the Cretaceous the geometry of the basin changed from a broad rift valley to a wide marine gulf and subsequently to a continental margin as pull-apart took place. The early Cretaceous consists of the lower South Perth Shale and the overlying Leederville Formation of interbedded sandstone, shale, siltstone and claystone, with minor conglomerate.

North of Perth the Leederville Formation is overlain by the Dandaragan Sandstone. An outcrop too small to map, which is possibly Leederville Formation, overlies conglomerate north-west of Walyunga (Wilde & Low 1978) and Fig. 9. Fluvial conditions persisted onshore and include the Bullsbrook Formation which was laid down
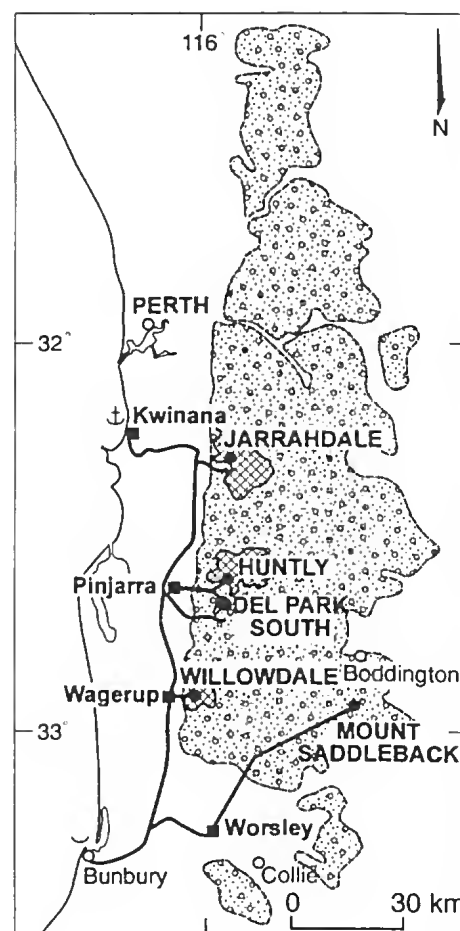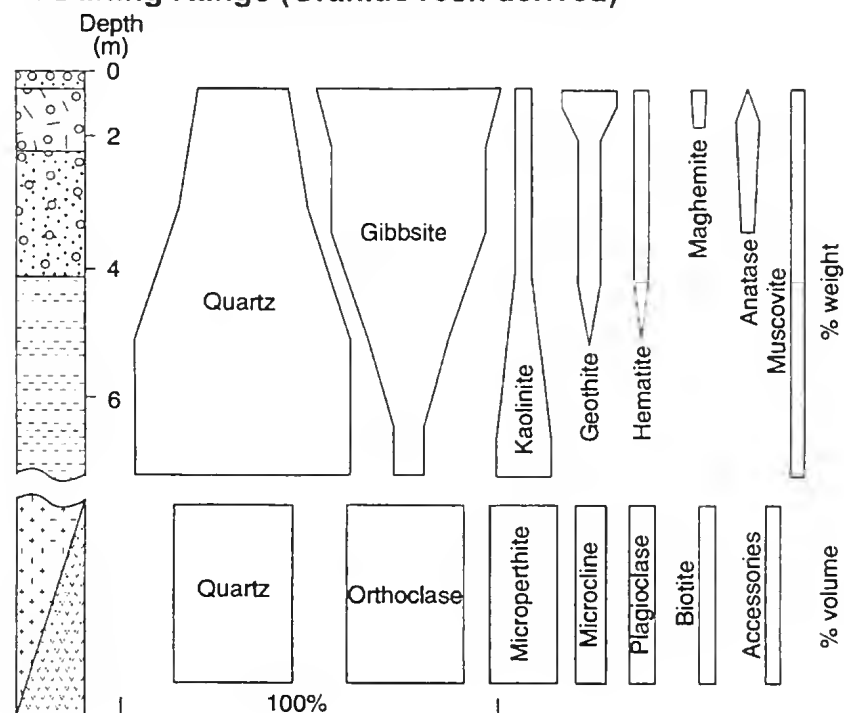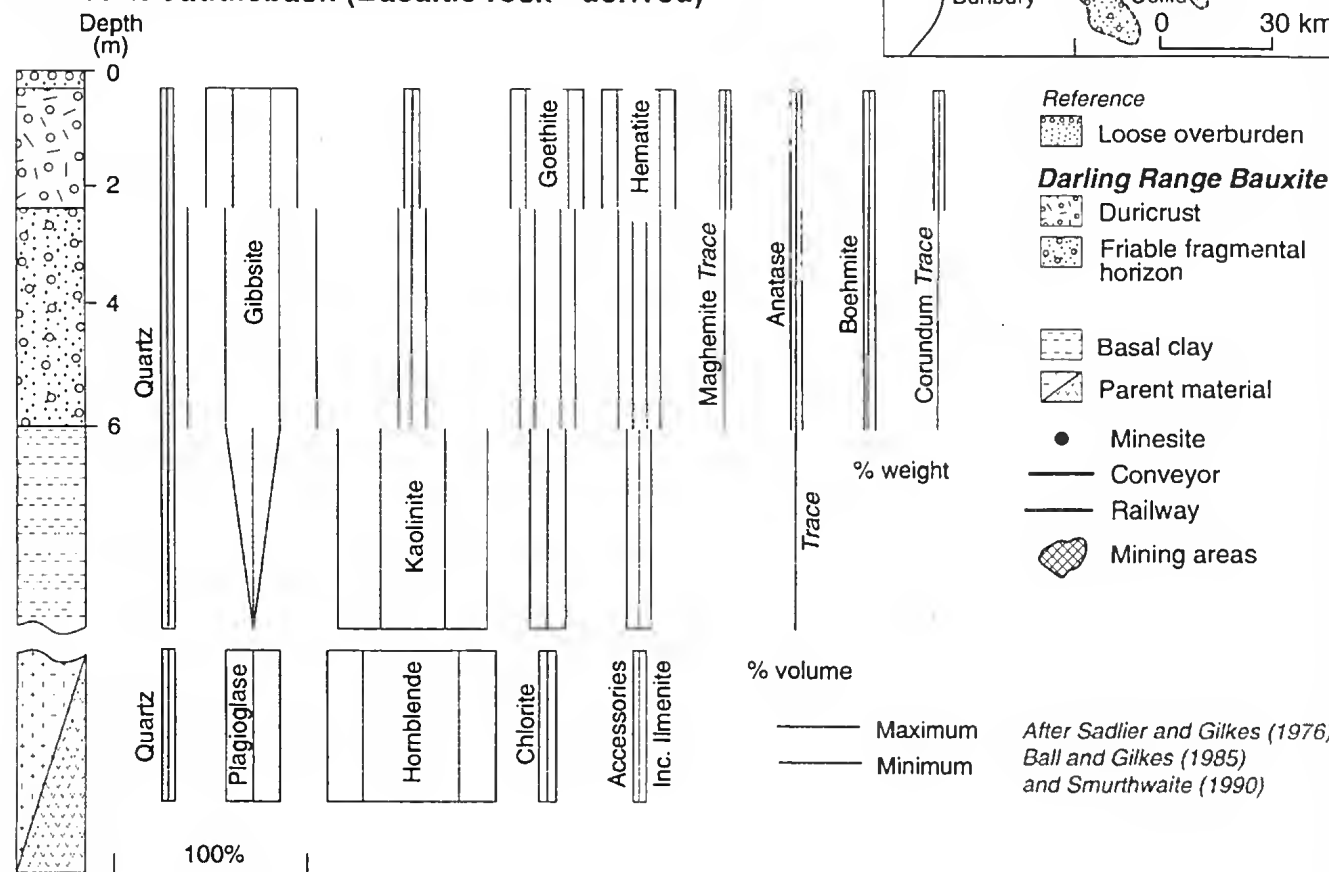
Figure 8. Locality map and typical profiles (from Sadlier & Gilkes 1976 and Ball & Gilkes 1985) through the Darling Range Bauxite.

Reference

Holocene

| Qra | Alluvial and colluvial deposits overlying bedrock at shallow depth. |

| Qrc | Sandy colluvial deposits of the western slopes. |

Pliocene-Pleistocene

| T-Qpa | Guildford Formation. Sediments of the alluvial fans, channels and flood plains of the Swan Coastal Plain. |

Pliocene

| Tpr | ? Yoganup Formation. Quartz sand with a basal conglomerate in places. |

| Tpj | Jumperdine Ferricrete. Ferricreted conglomeratic sand. |

| Tpw | Conglomeratic sand and conglomerate of the ancient Walyunga River. |

Eocene - Miocene

| Tgf | Greenmount Ferricrete. Massive, vesicular or pisolitic duricrust. |

Cretaceous

| Ko | Osborne Formation. Sandstone, siltstone and claystone. |

Palaeozoic

| Pwz | Playfair Weathering Zone. |

Archaean

| Age | Undifferentiated granitic rocks, overlain in places by clay, sand and boulders. |

| Am | Migmatite |

After Wilde and Low (1978)

Figure 9. The two classes of laterite (ferricrete), high-level and low-level, near Walyunga south-east of Bullsbrook. The east-west section follows Walyunga Road. The high-level ferricrete occurs across the Swan River at the Lookout.

in valleys cut into the Darling Scarp, as was the Donnybrook Sandstone to the south. After a brief regression, the sea returned to the Perth Basin and shallow-marine conditions prevailed for the remainder of the Cretaceous. Marine glauconite-bearing formations are predominantly Late Cretaceous. Movements on the Darling Fault ceased at this time, as Cretaceous rocks crop out a short distance east of the Darling Fault and in places may cap the Darling Fault itself.

South of Perth, Mesozoic units crop out on the Blackwood Plateau (Fig. 7). The "Maxicar Beds" (Lowry 1965; Playford & Low 1972) consist of 9 m of poorly sorted, ferruginous, feldspathic sandstone. Some sections are cross-bedded. Exposures of white claystone, siltstone and fine-grained sandstone 1 km north of the type locality, and of a siltstone and sandstone unit 4 km south of Burekup are included in the unit. J.M. Dickens, quoted

by Playford & Wilmott (1958), identified *Pterotrigonia* from the type locality.

The Arckaringa Weathering Zone

A distinctive pallid zone is developed in numerous "laterite profiles" along the south-west margin of the Australian Precambrian Shield, particularly where bauxite is present below the ferricrete and above the mottled zone. In these profiles (Figs 8 & 10), according to Smurthwaite (1990), the basal clay underlying the fragmental horizon (bauxite) is commonly mottled by iron staining in its upper parts (the San Marino mottled zone equivalent – later described – in the stratigraphy employed herein), but becomes more pallid with depth. It is commonly composed predominantly of clay particles, remnant quartz and partly weathered mica. This zone varies in thickness from 20–30 m before
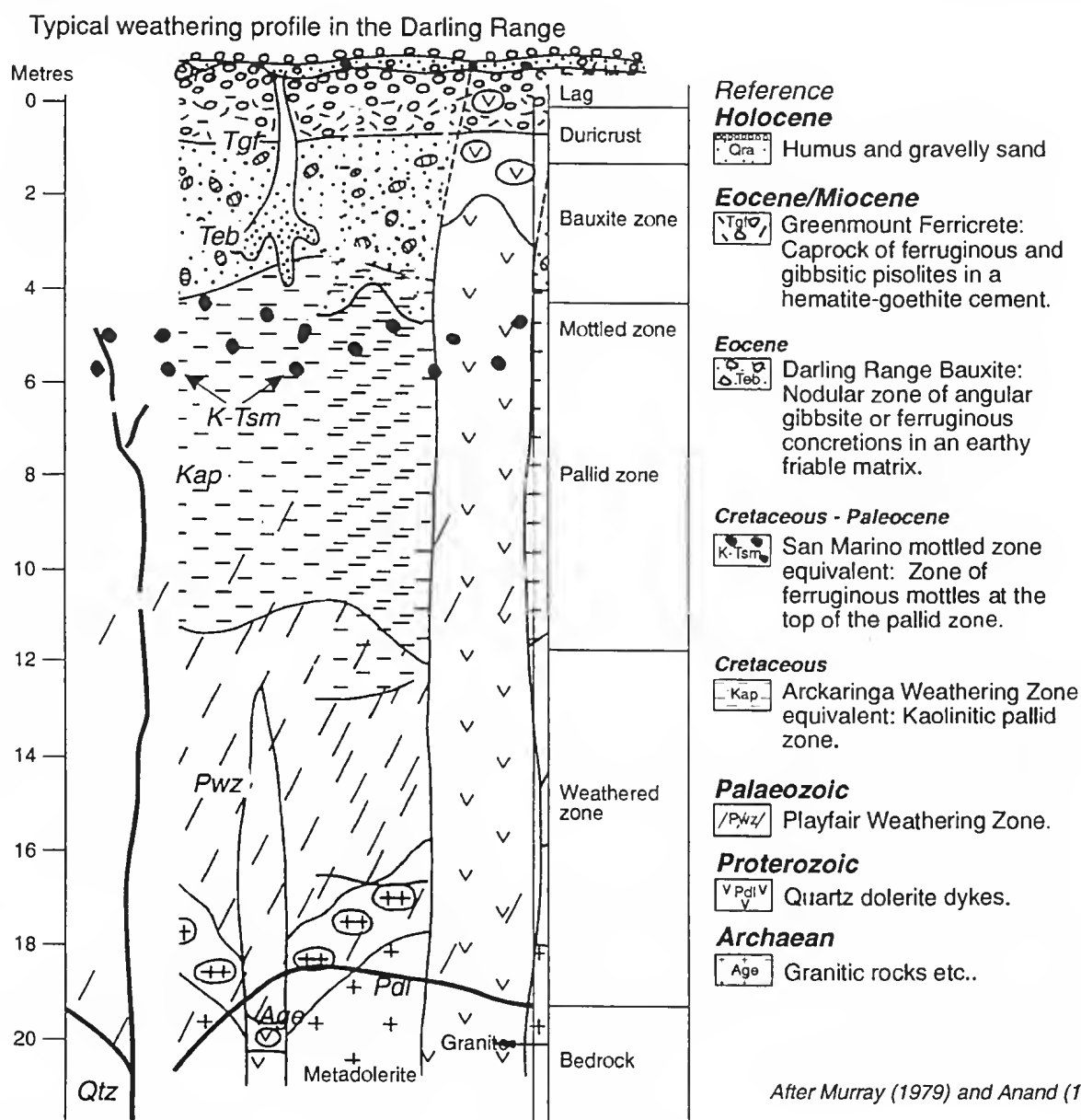
Figure 10. Typical weathering profile on the western margin of the Darling Range. Note the bauxite zone stratigraphically placed between the mottled zone and the overlying Greenmount Ferricrete (pisolitic nodular duricrust). This is a "high-level laterite profile". The weathered upper part of the Precambrian rocks intruded by a Proterozoic dyke has been assigned an age of Mesozoic (Kap, and K-Tsm) because this is the age of the weathered zone, and not the age of the basement rocks.

weathered bedrock, and then fresh is encountered. In some places the basal clay is absent below the bauxitic fragmental zone which rests directly on relatively unweathered bedrock in some places.

Silcrete profiles on the south-east margin of the Australian Precambrian Shield contain a pallid zone developed on previously weathered basement rocks in the uplands and on flat-lying sedimentary rocks of Mesozoic age within the Great Australian Basin (Wopfner 1964; Firman 1994); note that the term "Great Australian Basin" is used in preference to Great Artesian Basin, which has hydrogeological rather than stratigraphic connotations. The name Arckaringa Weathering Zone is derived from Arckaringa Homestead (Fig. 3). the type section is at Russo's Folly, an opal mine at Coober Pedy, where the pallid zone is developed in Cretaceous Bulldog Shale capped by younger beds (Firman 1980, 1994). The pallid zone has the consistency of stiff to hard clay or claystone.

The pallid zone is up to 30 m thick. North-east of Lake Eyre, where the zone is thinner, it is superimposed on an older, coloured weathering zone which itself is up to 24 m thick. In some places the Jurassic Algebuckina Sandstone separates the bleached sediments above from older weathered rocks below that unit so that the Arckaringa Weathering Zone is younger. Eocene Eyre Formation overlies the unit.

Near Adelaide, remnants of this ancient weathering zone are found overlying the Playfair Weathering Zone. Robertson (1974) has reported on this feature in the Verdun to Littlehampton Section of the South East Freeway where the material forms the pallid zone of a "Tertiary laterite profile".

The stratigraphic evidence suggests that development of the Arckaringa Weathering Zone, which post-dates some Late Cretaceous sediments and pre-dates early Cainozoic sediments, began in the Late Cretaceous.

The San Marino mottled zone

On the south-west margin of the shield, east of the Darling Fault, "laterite profiles" developed over basement rocks are exposed in many places (Figs 7 & 8). Although iron oxides are present in the mottled zone at the top of the Arckaringa Weathering Zone, they are not derived from the pallid zone, but are a groundwater feature developed below the eroded top. The mottled zone in these profiles is correlated with the San Marino mottled zone (the San Marino Palaeosol in Firman 1994). On the Dandaragan Plateau, in the north of the Study Area, Middle Jurassic limestones of the Cadda Formation and Champion Bay Group are leached and ferruginized in the weathered zone below ferricrete. On the Blackwood Plateau in the south the mottled zone in exposed Cretaceous "Maxicar Beds" near Dardanup resembles the San Marino mottled zone developed in Bulldog Shale and other Cretaceous sediments in the Great Australian Basin on the south-east margin of the shield, but the zone is not so well developed and may be younger.

Mottled zones and ferricretes associated with manganese deposits have been described by de la Hunty (1963) on the southern margin of the Pilbara Craton. The main area of outcrop is in the manganese province near Marble Bar. (Fig. 11). The oldest unit is the mottled zone found at a high-level in the landscape as an erosional remnant. This is capped in some place by a ferricrete and by younger units later described. The mottled zone is correlated herein with the San Marino mottled zone.

The San Marino mottled zone defined by Firman (1980, 1994) is exposed in the Stuart Range on the western margin of the Great Australian Basin. The name is derived from San Marino Homestead west of Oodnadatta on the headwaters of the Neals River, the type area for this unit (Fig. 3). The best exposures are found on higher ground on the margin of the basin. The unit is developed over a very wide area on an erosion surface at the top of early Cretaceous Cadnaowie Formation. Particularly good exposures are seen along Algebuckina Creek and near Coober Pedy.

The unit is characterized by ferruginous red or purple mottles developed in older materials. The individual mottles are up to 30cm across and in some places merge at the top of the zone of mottling to form a more-or-less continuous ferricrete. Similar ferruginous accumulations have been described elsewhere on the south-east margin of the Australian Precambrian shield by Reyner (1955), Coats (1963), and Wopfner (1964). Where ferruginous mottles occur in silcrete profiles the mottles below and close to the silcrete are silicified in many places. There are some sequences – near Coober Pedy for example – where ferruginous mottles are developed in Tertiary sediments overlying the San Marino mottled zone, but this mottling is not affected by silification and marks a younger period of ferruginous accumulation. The oldest sediments unaltered by formation of mottles of this kind and overlying the zone are part of the Miocene Edadunna Formation.

Idnurm & Senior (1978) have carried out palaeomagnetic dating of ferruginous material in profiles that are morphologically similar to those investigated by Firman (1980) in an adjoining area in the Great Australian Basin (Fig. 3). The kaolinitic Morney Profile developed in the Cretaceous Rolling Downs Group is similar to profiles containing the San Marino mottled zone developed in Cretaceous Bulldog Shale. A late Cretaceous (Maastrichtian) to Early Eocene age was determined for the ferruginous material in the Morney profile, which indicates that the San Marino mottled zone post-dates the Arckaringa weathering zone.

Stratigraphic relationships indicate a Late Cretaceous to Paleocene age for the San Marino mottled zone.

Early and Middle Cainozoic – marine sediments, bauxite, ferricrete and silcrete

In this part of the text new names are introduced for ferricrete and silcrete on the western margin of the shield. The geological setting for ferricretes and silcretes on the south-east margin of the shield is outlined in the references quoted.

Early Cretaceous in the Perth Basin is represented by Leederville Formation on the Dandaragan Plateau, by the Donnybrook Sandstone on the Blackwood Plateau, and by the Leederville Formation (underlying the Late Cainozoic sediments) in the central Swan Coastal Plain.
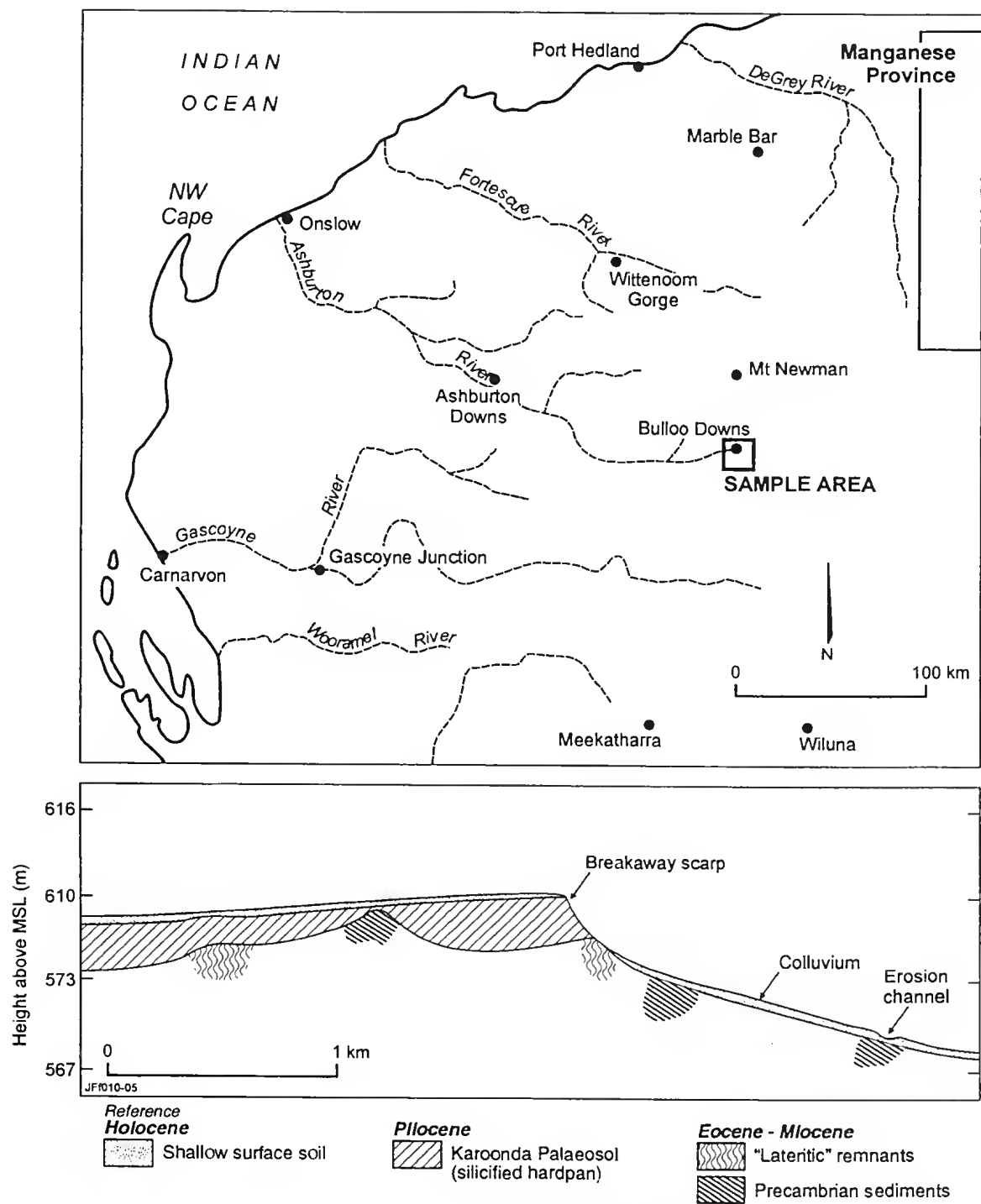
Figure 11. Karoonda Palaeosol near Bulloo Downs and the Pilbara (Goldfield) Manganese Province. The section is diagrammatical and no R.F. is available. The boxed area to the NE is the Manganese Province.

The apparent displacement, which is said by Finkl & Fairbridge (1979) to be due to downwarping, is marked by structural lineaments which, from north to south, control the Gingin Scarp, the Darling Scarp and the Whicher Scarp along the western margin of the Blackwood Plateau.

Paleocene and Eocene sediments

Throughout the Cainozoic, the Perth Basin was on the continental margin bordering the Indian Ocean, with a shoreline which fluctuated between the shelf edge and the Darling Scarp. Foraminifers indicate an Early Cretaceous to Late Paleocene age for these sediments. The ancestral Swan River cut a deep valley into the underlying sediments in the Perth region. This valley may once have connected with the Perth canyon, which now cuts the continental slope west of Rottnest Island. Sea-level rose and fine-grained quartz sands (the Kings Park Formation of Late Paleocene to Eocene age) were laid down in the drowned river valley.

Crustal thinning and downwarping led to separation of the southern margin of Australia from Antarctica and the creation of the Southern Ocean during the Eocene. Emergence took place during the Early Eocene. Following a brief interval of erosion the sea again covered the continental shelf and another cycle of shallow-marine carbonate sedimentation took place.

The Kojonup Sandstone, a quartz sandstone overlying a thin basal conglomerate of Eocene age (Wilde & Backhouse 1977), directly overlies Precambrian granite rocks to the south and south-west of Kojonup. The unit contains the plant fossils *Araucaria*, *Nothofagus*, *Ficus* and *Banksia* similar to those found around the Stirling Range. Similar fluviatile sandstone extends for 380 km north to the vicinity of Calingiri, but the sandstone in that area may be younger.

The Darling Range Bauxite

Alumina-rich clay occurs along the south-west margin of the Australian Precambrian Shield in residual deposits associated mainly with Archaean granite and migmatite and doleritic bedrock. The name "the Darling Range Bauxite" is commonly used in the literature for bauxite deposits in the south-west of Western Australia (Darling Range is used herein for the south-west margin of the Australian Precambrian Shield marked by exoreic drainage). These bauxite deposits extend along the Darling Range from the Bindoon-Chittering area in the north through Jarrahdale and Pinjarra to Wagerup south, and east to Mount Saddleback, where metamorphosed basalt is the parent material (Figs 7 & 8). The name Darling Range Bauxite is used herein for the bauxite ore including the lowermost gibbsite horizon in sections described as *in situ* by Hickman et al. (1992).

Smurthwaite (1990) states that the bauxite deposits of the Darling Range occur as lenticular ore bodies within a "laterite profile". These profiles consist of four layers: overburden, duricrust (ferricrete or bauxitic ferricrete herein), friable fragmental horizon and basal clay. The lowermost fragmental horizon is the original bauxite, the younger layers consist of material reworked from the lower fragmental unit. The upper part of the friable unit is characterized by nodules of gibbsite, which decrease in concentration below the unit. The basal clay is commonly mottled by iron staining in its upper parts, as in the San Marino mottled zone of the Great Australian Basin discussed earlier, but becomes more pallid with depth in the Arckaringa weathering zone.

Grubb (1971) has described several profiles in the bauxite deposits at Jarrahdale. In the Seldom Seen open-cut only two profiles are of *in situ* eluvial or residual bauxite, four profiles show varying degrees of erosional redistribution. The *in situ* profiles are composed of four horizons. From top to bottom these are: fine uniform pisolitic bauxite often showing significant surface hardening, a coarser unconsolidated pisolitic zone, a very coarse concretionary zone ferruginous in many places, and mottled and pallid clay, a "...distinctive basal horizon which underlines all true laterites". Hematite is characteristic of the hardcap in these profiles. Brimhall & Lewis (1992) have shown that the mineral framework of the hardcap (the Greenmount Ferricrete – later described) contains small rounded grains of zircon. Ore thickness over granitic bedrock ranges from 2 to 7 m. In the Mt

Saddleback region, bauxite ore is generally 6–7 m thick and locally attains a thickness of 20 m (Hickman et al. 1992).

Grubb (1971) was of the opinion that the bauxite deposits of the Darling Range began with reconstitution of a colluvial mantle to form fluvial sediments during the Cretaceous. Intense leaching of kaolinite and halloysite may have followed an elevated ground-water table during the Middle Eocene high sea and formation of gibbsite in favourable areas during the world-wide drop in sea level that followed..

The friable fragmental unit in the bauxitic deposits of the Darling Range is stratigraphically placed between the Late Cretaceous-Paleocene San Marino mottled zone and the Eocene-Miocene Greenmount Ferricrete next discussed. An Eocene age for the Darling Range Bauxite is suggested.

In Western Australia, the relationship of basement rocks to the geochemistry of typical bauxite profiles has been discussed by Baker (1975), Sadlier & Gilkes (1976), Gilkes & Suddhiprakarn (1981), Ball & Gilkes (1985) and Anand et al. (1991).

On the south-east margin of the shield at Pidinga Lake, about 80 km north-west of Chundie Swamps (Fig. 3; and Firman 1985) alunite has been formed in sediments at the top of Paleocene-Eocene Pidinga Formation. King refers to the localization of alunite – now beneath younger "lateritic cappings" – and claims that impeded drainage resulted in the formation of alunite rather than gibbsite. At Chundie Swamps Pidinga Formation is overlain by silcrete and the younger Miocene Nullarbor Limestone.

The Greenmount Ferricrete

There are two classes of laterite (ferricrete) according to Simpson (1912), the primary or "high-level laterite" and the secondary or "low-level laterite" composed largely of mechanically transported fragments derived from the "high-level laterite". Near Perth the "high-level laterite" is about 215 m above sea level and the "low-level laterite" about 80 m above sea level (Figs 7 & 9).

"High-level laterite" was used by Simpson (1912) to describe ferricrete – "pisolitic" in many places – as in the giant laterite profile shown on Figure 10. This material was called ironstone by early explorers in Western Australia. The ferricrete associated with other sediments in many places around the southern coastal margin is an iron cemented sedimentary sandstone.

Prider (1948) has described laterite (ferricrete) in the Ridge Hill Shelf area near Perth and his work forms the basis for the description and formal definition of the older high-level Greenmount Ferricrete, now described, which is named after Mount Helena, and the younger Jumperdine Ferricrete described later. Prider (1948) states that the "high-level laterite" varies in character according to the nature of the underlying Precambrian rocks. All the "high-level laterites" are underlain by a highly weathered (kaolinized) zone which passes down into the unweathered country rock, as described by Simpson (1912).

In the Perth area, Wilde & Low (1978) state that laterite (ferricrete) is generally massive and well-cemented, and may be pisolitic. It is about 4 m thick and overlies a pallid

zone of variable thickness and weathered bedrock. Although there are many sections through these profiles where the ferricrete is only about 1 m thick, it has an average thickness in the Pinjarra area of 4–5 m and a 14 m thickness at Del Park near Pinjarra (Fig. 7). A supplementary section is proposed for the Greenmount Ferricrete at Coates Siding about 50 km north-east of Perth near the Great Eastern Highway.

Vesicular and pisolitic laterite (ferricrete) as a caprock is recorded in the Moora area on the Dandaragan Plateau by Carter & Lipple (1982). Wilde & Low (1978) have recorded "strongly lateritized" glauconitic greensand (Poison Hill Greensand) of Cretaceous age cropping out at Poison Hill (31° 18′ S 115° 53′ E, 7.5 km north-west of Gingin). In the Gingin – Mooliabeenie area (Firman 1952), the eroded top of the Late Cretaceous Poison Hill Greensand slopes down to the west between the Darling Fault to the east and the Gingin Scarp to the west. The greensand – and other quartz sand of uncertain age on the eastern margin of this area – is heavily ferruginized in the high-level laterite (ferricrete) which extends to the west from the Australian Precambrian Shield.

On the Blackwood Plateau a massive high-level laterite (ferricrete) is correlated with that on basement rocks to the east of the Darling Fault described by Finkl (1971). The ferricrete is generally quartz-rich, reflecting the composition of the bedrock. Near the western margin, it is bounded by distinct breakaways.

On the Pilbara Craton north of the study area, de la Hunty (1963) refers to scattered outcrops of a ferricrete which forms a caprock on the mottled zone. Manganese oxides overlie the ferricrete in some places. The caprock is correlated herein within the Greenmount Ferricrete of the Darling Range to the south and the Yallunda Ferricrete on the south-east margin of the shield.

Finkl & Fairbridge (1979) assumed that the laterite (ferricrete) in Western Australia was due to desiccation in the Oligocene after marine regression in the Eocene. Woolnough (1918) suggested a Miocene age.

On the south-east margin of the Precambrian Shield, mottled zones and ferricrete – the Yallunda Ferricrete (Firman 1967b) – were formed on old land surfaces in the upland areas marginal to the southern sedimentary basins where they occur at the top of assemblages of materials in "laterite profiles". Ferruginous accumulations described by other investigators and attributed to the Yallunda Ferricrete by the writer have been recorded by Firman (1994). The Yallunda Ferricrete is developed over sediments of Paleocene to Eocene age – Pidinga Formation and equivalents on the coastal margin and Eyre Formation inland – and is overlain by sediments of Oligocene to Miocene age – Nullarbor Limestone on the coastal margin and Etadunna Formation inland.

In the Mount Lofty Ranges near Adelaide, The Yallunda Ferricrete occurs as remnants of an extensive sheet of ferricrete overlying the Playfair Weathering Zone. The zone was developed below a surface formed over Proterozoic, Cambrian and Ordovician rocks moderately folded in the Delamerian Orogeny. Hard pisolitic ferricrete closely resembles that of the Mount Helena Ferricrete on the western margin of the shield in the Darling Ranges near Perth.

The pisolitic ferricrete near Adelaide is correlated with the stratigraphically bracketed ferricrete within the Middle Eocene sequence exposed on the coastal margin at Witton Bluff near Christies Beach in the St. Vincent Basin as described by Glaessner & Wade (1951).

The ferruginous sandstones overlying alunite of Eocene age at Pidinga Lake and Chundie Swamps on Eyre Peninsula – previously described in relation to the Darling Range Bauxite – are probably of the same age as the ferruginous non-marine sandstones in the Mt. Lofty Ranges near Adelaide.

Oligocene and Miocene sediments

During the Oligocene and Miocene, the geometry of the Perth Basin was similar to that of the present day. The Oligocene and Miocene sequence rests disconformably on the Paleocene and Eocene sequence in the offshore basin, and unconformably overlies the Permian sequence onshore. The Stark Bay Formation and Victoria Plateau Sandstone are the only named formations. The sequence is 230 m thick. West of Perth, the sequence is less than 20 m thick. Fossils include foraminifers, bryozoans and echinoderms and the former suggest an Early to Middle Miocene age. Where carbonates have been sampled they are a friable white, bryozoan and echinodermal calcarenite, with brown dolomite and chert.

In South Australia – in the Murray Basin – pisolitic "ironstone gravel" is found in the Oligocene Compton Conglomerate (Firman 1973).

Palaeomagnetic dating of ferruginization in the kaolinitic Canaway profile in the Cretaceous Rolling Downs Group of southwest Queensland (Idnurm & Senior 1979; Senior & Mabbutt 1979), indicates an Oligocene to Miocene age.

The Calingiri Silcrete

Silicified rocks are widespread on the Australian Precambrian Shield and in adjoining basins. Stephens (1971) shows that silcrete profiles dominate in the Canning, Officer and Great Australian basins (Figs 2 & 3). In those regions, older ferricrete profiles have been partially eroded prior to development of the silcrete. Uplift produced topographic features showing inversion of relief and an abundance of silcrete at high levels in the landscape. Pliocene sediments occupy a lower position in the landscape.

The Calingiri Silcrete has been described by Wilde & Low (1978) as a unique deposit, which occurs 6 km south of Calingiri (Fig. 12). This is the type area for the silcrete. The silcrete is a subhorizontal flaggy unit that contains large quartz and kaolinized feldspar fragments in a cemented sandy matrix, and is associated with sand rich in quartz cobbles. The deposit has been ferruginized in part. It occurs on the drainage divide between the Moore, Avon and Mortlock river systems and may represent a pre-Pleistocene drainage system. The silcrete caps a fluvial sequence of fine-grained quartz sand overlying well-rounded conglomerate at the base. The original cap may have been no more than a metre thick. The sand below the silcrete has been strongly cemented by silica. The deposit, which occurs in many places at elevations above modern drainage patterns, records an inversion of

Reference

Holocene

| Qra | Alluvium. Clay, sand and loam. |

| Qsp | Thin-bedded quartz sands and ferruginous pisolites overlying Archaean granite rocks. |

Pliocene

| Tpj | Jumperdine Ferricrete. |

Miocene

| Toc | Calingiri Silcrete. Flaggy silcrete developed in Oligocene-Miocene quartz sands with basal boulder beds. |

Archaean

| Am | Migmatite. |

| Anb | Quartz-feldspar-biotite gneiss. |

After Wilde and Low (1978)

Figure 12. Occurrence of the Calingiri Silcrete 6 km south of Calingiri, the type area for the silcrete.

relief. This unit crops out discontinuously as far south as Muradup near Kojonup (Fig. 7) and may be as old as the Kojonup Sandstone which has sediments of Eocene age at the base (Wilde & Walker 1982), but may itself be younger. The silcrete cap is a hard dense silcrete found at the top of the sequence as large tabular boulders.

Silcrete of uncertain age has been reported from the other areas in the southern part of Western Australia: Silcrete described as small patches of pale grey, porcellanitic conglomerate up to 5 m thick is recorded in the Moora area (Carter & Lipple 1982). Wilde & Walker (1982) refer to the Greenbushes Formation which is also cemented by silica. Palaeodrainage deposits extending in

a discontinuous arc from Salmon Gums to Cundeelee are outlined by undulating duricrust surfaces at high level and chains of playa lakes (Hocking & Cockbain 1990). Hill cappings of silcrete with laterite (ferricrete) on lower slopes and valley floors are recorded elsewhere on the Yilgarn Craton by Hocking & Cockbain (1990). This suggests a topographic sequence with older materials at high level, a common feature of terrain in this area. The ferricrete at lower level could be the younger Pliocene Jumperdine Ferricrete later described.

On the Pilbara Craton, silcrete is widespread on the plateau near the junction of the Oakover and Davis rivers, which are tributaries of the De Grey River

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(de la Hunty 1963). The silcrete was developed on an erosion surface from which other surficial materials have been removed to expose dolomites and other rocks of the Proterozoic succession.

The Calingiri Silcrete is probably of Miocene age, which is in agreement with the suggestion of Butt (1985), that silcrete on the Yilgarn Craton is of Oligocene to Middle Miocene age.

The Clayton River Silcrete on the south-east margin of the shield (Firman 1980, 1994) occupies a similar stratigraphic position to the Calingiri Silcrete. On the south coast margin, silcretes of Miocene age have been recorded at Wallaroo (Lindsay 1970) and Chundie Swamps (Firman 1983), where silcrete overlies Eocene Pidinga Formation and is overlain by Miocene Nullarbor Limestone. Inland the Clayton River Silcrete is developed on Eocene Eyre Formation and is overlain by Oligocene-Miocene Etadunna Formation. In the inland the Arckaringa Weathering Zone is found below the silcrete. Silcrete of Miocene age has been recorded by Barnes & Pitt (1976) which contains reworked silcrete clasts, and by Ambrose & Flint (1981) who have also described syndepositional silcrete south-west of Lake Eyre (Fig. 3).

A sequence of separate events can be interpreted from the silcrete profile: this includes – from oldest to youngest – bleaching of pre-existing fine-grained rocks, development of a clastic mantle, formation of ferruginous mottles, erosion of ferruginous duricrust and impregnation of the clastic mantle and underlying mottled zone with silica to form a silcreted clastic mantle overlying a "porcellanized" siltstone (Fig. 13).

Important references dealing with silcrete profiles in South Australia are those of Milnes *et al.* (1985), Wells & Callen (1986), and Drexel & Preiss (1995), the latter prepared subsequently to Firman (1994).

Late Cainzoic – sediments, pisolitic deposits, siliceous pans and mottled zones

Tectonic activity beginning in the Miocene led to the break-up of Tertiary basins in southern Australia and to the elevation of the ranges on the basin margins. The western margin of the Dandaragan Plateau, the Precambrian Shield in the Perth area and the Blackwood Plateau have been eroded during a high stand of the Early Pliocene sea to form the Ridge Hill Shelf which extends from Eneabba in the north to Tutunup in the south. The oldest of a sequence of strandline deposits, some with heavy-mineral sands, occurs along the scarp up to 130 m above present sea-level.

Pliocene sediments

The Pliocene sequence probably occurs throughout the offshore Perth Basin. It is widespread onshore where it occurs across the basin as far as the Darling Scarp. The sequence rests disconformably on Oligocene to Miocene sediments offshore, and unconformably overlies the earlier, mainly Mesozoic, sequences onshore. The Pliocene sequence includes all of the late Cainozoic stratigraphic units assigned to the Wadjemup, Yoganup and Ascot formations in the Perth Basin. The sequence consists predominantly of medium to coarse-grained sand with lenticular beds of clay and conglomerate.

Shells, especially molluscs, are abundant in some units and are the basis for dating the sequence as late Cainozoic (Cockbain 1990).

Near Perth, at Walyunga (Fig. 9), conglomeratic sediments are unconformably overlain by the Jumperdine Ferricrete. The conglomerates may be coeval with similar deposits described by Churchward & Bettenay (1973) and named the Harvey Formation in Hocking & Cockbain (1990), and also the Kirup Conglomerate near Mullalyup, although this may be older (Finkl & Fairbridge 1969). These deposits mark prior streams at a high level along the scarp which post-date the Eocene – Miocene Greenmount Ferricrete and pre-date the Guildford Formation equivalents at lower levels in adjoining valleys.

In the Pinjarra area isolated patches of sand at elevations of 75–90 m above sea-level have been recorded by Wilde & Low (1980). They describe the sediments as bleached shoreline sand with a thin basal conglomerate. The sand deposits in the Pinjarra area are possibly equivalent to the beach and dune sand, with local concentrations of heavy minerals, found along the Happy Valley Shoreline of Welch (1964) and Wilde & Walker (1982). In the Collie area, conglomerate, sand and clay occupy the highest position in the landscape. The sediments overly strongly silicified Kojonup Sandstone and have a "lateritic hardcap" (Wilde & Walker 1982).

The Jumperdine Ferricrete

The Jumperdine Ferricrete has its clearest geomorphological expression along the Ridge Hill Shelf on the western margin of the Australian Precambrian Shield. The Jumperdine Ferricrete is named after Jumperdine Creek south-west of Calingiri (Figs 7 & 13). The type area is at Ridge Hill south of the Helena River valley in the Perth area. The description follows Prider (1948): the low-level laterite (ferricrete) occurs as a thin discontinuous layer above ferruginous sandstone (The Ridge Hill Sandstone of Mesozoic age; pers comm. Professor Simon Wilde 2005). It has, on the exposed surface, a somewhat fragmental appearance, but on breaking the rock these fragments are seen to be of ferruginous sandstone. These fragments in a typical specimen average 5 mm diameter and are coated with a dense layer of light brown, fine-grained and compact bauxitic material and the spaces between the fragments are largely filled with this bauxitic material, but some cavities remain giving the rock a slightly cellular structure. The surface "lateritic" crust passes down into ferruginous sandstone at about one metre below the ground surface.

Along the Ridge Hill Shelf the Jumperdine Ferricrete overlies weathered bedrock, unweathered bedrock or younger sedimentary rocks. The development of the unit over sedimentary rock interposed between weathered bedrock below and the ferricrete demonstrates that the ferricrete is not genetically related to the underlying weathered bedrock. The ferricrete has been interpreted as a deposit which contains reworked ferruginous and bauxitic material derived from the older high-level laterite profile adjoining to the east.

In the present interpretation, the low-level ferricrete post-dates the high-level Eocene-Miocene Greenmount Ferricrete and pre-dates the Pliocene Yoganup Formation
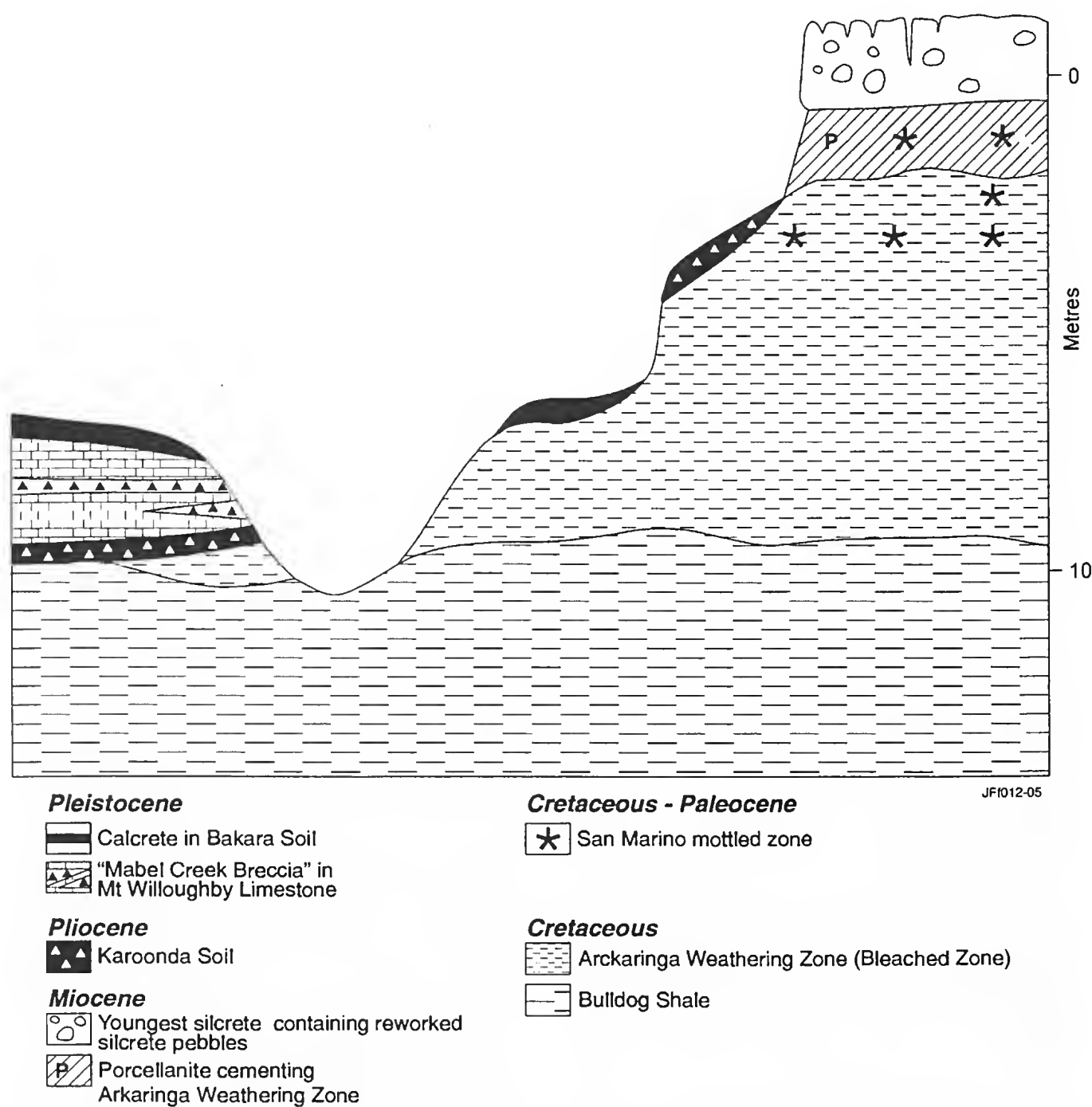
Figure 13. Silcrete near Wurdlata west of Coober Pedy in South Australia. The right hand sequence is a typical silcrete profile in the Great Australian Basin. It contains pebbles of older silcrete and is typical of silcretes in palaeochannels in the region. The left hand sequence of younger pedocretes and sediments is unusual in that a number of surfaces converge at the one site.

found at a lower level at the base of the Gingin, Darling and Whicher scarps on the eastern margin of the Swan Coastal Plain. A Pliocene age is suggested for the Jumperdine Ferricrete.

There are other localities along the Darling Scarp north of Perth where the ferricrete occurs: approximately 280 km north of Perth in the High Hill – Mt Lesueur area overlooking the Hill River; from about 130 km north of Perth near Two Brooks Park along the Brand Highway to the high ground east of Cervantes; and at Gingin 76 km north of Perth in the valley of an antecedent stream deeply incised into the Cretaceous marine sequence and

now occupied by Gingin Brook (Fig. 7). Wilde & Low (1978) describe a "partially lateritized" gritty sandstone at the head of present drainage channels in the Calingiri area east of the Ridge Hill Shelf. This is the Jumperdine Ferricrete described earlier and overlying the Calingiri Silcrete south of Calingiri.

Near Perth the Jumperdine Ferricrete occurs at Walyunga (Fig. 9) where it overlies conglomeratic sediments unconformably. The Jumperdine Ferricrete also caps sandy valley fill along Good's Road South of The Lakes on the Great Eastern Highway. At the last-named site the ferricrete is below the level of the

Greenmount Ferricrete, and the sediments underlying the ferricrete cap have been derived by erosion of the Playfair Weathering Zone from the adjoining uplands.

Crudely bedded pisolitic ferricrete re-worked from the Mount Helena Ferricrete and now weakly cemented occurs near 'Yalanbee" Experiment Station (Anon 1993). This also may be Jumperdine Ferricrete.

Along the Whicher Scarp a distinct bench at about 80 m above sea-level is in the same topographic position as the Ridge Hill Shelf. The bench is "lateritized" and there is a local concentration of heavy minerals. Elsewhere on the Blackwood Plateau a dissected "lateritized bench" at the heads of the valleys rising upstream from 80 m to 130 m above sea level has been recorded (Wilde & Walker 1982).

On the south-east margin of the Australian Precambrian Shield, ferruginous sediments were deposited and now form caprocks over weathered Proterozoic rocks at the "Gun Emplacement" near Adelaide, and over the Hallett Cove Sandstone (Firman 1994). In the Murray Basin ferruginous caprocks were formed on late Pliocene sediments including the Loxton Sand and the Diapur Sandstone. In the Murray Basin the fossiliferous Norwest Bend Formation, which is coeval with the uppermost Parilla Sand, marks a high stand of the late Pliocene Sea in the same way as the Yoganup Formation in the Perth Basin on the south-west margin.

Ferruginous and siliceous deposits formed below the level of older deposits stranded in the uplands and overlying the older deposits within the basins have been discussed by Coates 1963, Freytag et al. 1967, and Forbes 1975.

Pliocene sediments and the Robe Pisolite

Deposits of pisolitic limonite (the Robe Pisolite) have been described by de la Hunty (1965) in the Mt Bruce area north-west of Newman in the Pilbara region. The unit, which consists of close-packed iron oxide cemented pisolites with bands of more massive goethite is up to about 50 m thick in places, can be traced along palaeovalleys for up to 80 km in the Hamersley Basin. Black shales underlying the unit contain spores and pollens of Eocene age (Blockley 1990). In many places older laterite and silcrete profiles are found at a high level in the landscape, and the younger pisolitic deposits in the lowlands are overlain by calcrete.

A more appropriate name for the Robe Pisolite is 'Robe Formation' because the unit is lithologically diverse. Basal parts of the unit are chiefly massive goethite and upper parts typically range from oolitic goethite to mixed oolitic – pisolitic goethite to pisolitic goethite (D.K. Glassford per comm 2005).

Deposits similar to the Robe Pisolite form part of the Doonbara Formation in northern South Australia. Doonbara Formation was defined near Cordillo Downs Homestead in the north-east of South Australia in the Great Australian Basin by Wopfner (1974). A red ferruginous sandstone overlain by the Karoonda Soil – later described – was recorded by Forbes (1969) and Firman (1994) on the south-west margin of the basin near Kingoonya and was assigned to this unit. Forbes (1977) also describes the sandstone in the Tallaringa area, west of Coober Pedy (Fig. 3), where it overlies the Avondale

Clay. On the south-east margin of the shield the Avondale Clay is an important Pliocene sequence. It is described briefly because it helps to define the stratigraphic position of Doonbara Formation, which includes pisolitic ironstone resembling the Robe Pisolite in Western Australia.

The Avondale Clay (Firman 1967a) is a grey clayey sand. It contains vertically oriented ferruginous patches and mottles which in some places are lithified. Outcrops – base not exposed – are up to 10 m thick. The type section is on the plateau margin north of Leigh Creek (Fig. 3) near Mt Playfair and 2 km south of Lyndhurst. The unit crops out near Lake Frome at Mulligans Hill. At Lake Eyre North, a possible equivalent of Avondale Clay is underlain by a sequence of dolomite and mudstone (King 1956). Similar sequences in Lake Palankarinna and Lake Kanunka named the Etadunna Formation (Stirton & Tedford 1961) contain the Ngapakaldi Fauna of pelicans, flamingoes, ducks, crocodiles, lungfish and an ancestral koala of Oligocene to Miocene age. P.A. Rogers (pers.comm 2002) correlates the Namba Formation of Callen & Tedford (1976) at Lake Palankarinna with Avondale Clay.

At least 140 m of sediment was recorded near Port Augusta at the head of Spencer Gulf by Hullett, 1882 (Firman 1965). The uppermost is assigned to the Hindmarsh Clay, a stratigraphic equivalent of Guildford Formation in south western Australia described later. The lower part of the sequence contains Avondale Clay and is underlain by lignitic clays and carbonaceous sands that may be of Eocene age. The position of the boundary between Avondale Clay and the underlying lignitic clays and carbonaceous sands is not known. Avondale Clay also occurs on Yorke Peninsula at Wallaroo where it underlies Hindmarsh Clay.

The Doonbara Formation in northern South Australia and the Robe Pisolite in the Pilbara area, are both overlain by limestones with opaline silica at the top: The Mt Willoughby Limestone (Nichol 1971) and some other limestones in northern South Australia described by Wopfner (1974) are assumed to be the stratigraphic equivalent of the Oakover Formation in the Pilbara area.

Palaeomagnetic dating of ferruginous material in Doonbara Formation suggests a Miocene to Pliocene age for the unit (Indurm & Senior 1978).

Sediments of Pliocene – Pleistocene age

Non-marine sediments of Late Pliocene-Pleistocene age are host rocks for palaeosols in sequences on the south-west and south-east margins of the Australian Precambrian Shield. The sediments are sandy clays and clayey sands with ferruginous mottles and gravels which together form alluvial fans and piedmont slope deposits. Most of the clay deposits of this age have well-developed soil structures.

In the Perth Basin (Fig. 2) west of the Ridge Hill Shelf, the material of fans, channels and flood plains was named the Guildford Formation (Baker 1954; Low 1971). The sediments of the Guildford Formation are interbedded alluvial clays and sands with thin lenses of basal conglomerate according to Wilde & Low (1978).

The type section of the Guildford Formation is in the west Guildford artesian bore (lat.31° 54' 30" S, long. 115°

57' 20" E) from the surface down to 32.99 m (Low 1971). The unit includes a thin bed containing marine fossils (*Anadara, Dosinia,* etc), at a height of about 4.5 m above low-tide level in the brick clay pits at Caversham (lat. lat.31° 53' 5" S, long. 115° 58' E). The fossiliferous bed and the overlying units including gypsiferous material are possibly much younger than the clays of the underlying formation (Teichert 1967; Gill 1974).

The thickness of the sequence rarely exceeds 100 m. It unconformably overlies the Early to Late Cretaceous Osborne Formation, the Late Cretaceous Leederville Formation, the Late Paleocene to Eocene Kings Park Formation and the Late Pliocene Yoganup Formation elsewhere below the coastal plain. The unit is overlain by late Cainozoic alluvium and marine and aeolian sediments of the Kwinana Group within the Perth Basin.

The younger beds of Guildford Formation are exposed in irrigation channels near Mundijong (Fig. 7) where the lowest unit is a stiff to hard, light grey, clayey sand or sandy clay with coarse dark red and yellow mottles. Older mottled clays and sands are exposed in deep pits in the piedmont zone and on the walls of the Murray River valley near Avondale Homestead where they are overlain by yellow clay of the soil system known as Boyanup Loam. Similar deposits occur inland near Boorabbin on the Great Eastern Highway (Stop 2 in the Excursion Guidebook prepared for the International Conference on Desert Landscapes and IGCP252 by Glassford & Semeniuk 1991). The Guildford Formation is the oldest known part of the sequence of fans, channel and flood plain deposits developed west of the Darling Scarp following the retreat of the shallow sea marked by Yoganup Formation. The exposed part of the sequence is separated into upper and lower beds by "siliceous and silicified rock" (McArthur & Bettenay 1960).

On the south-east margin of the Australian Precambrian Shield, Late Pliocene-Pleistocene non-marine sediments crop out which are stratigraphic equivalents of the Guildford Formation. These include clays and sands on the shield itself, clays and sands in alluvial fans flanking the central ranges, and lacustrine and fluvial sediments within Tertiary basins.

Palaeontological investigations summarized in Firman (1976) show that the youngest clays and sands exposed at ground surface along the southern coastal margin are of Pleistocene age. These deposits rest upon clays and sands within Tertiary basins which palaeomagnetic studies of the Blanchetown Clay and associated sediments in the Murray Basin show extend back into the Late Pliocene (An *et al.* 1986).

The Karoonda Soil

The Karoonda Soil (the Karoonda Palaeosol of Firman 1988) is a prominent feature in alluvial fans on range margins and in sedimentary basins where it is associated with coastal and non-marine clays and sands of late Pliocene age (Firman 1994). It marks the Karoonda Surface of Firman (1966, 1969a). Inland, it is developed on older rocks and commonly occurs as ferruginous clasts cemented by silica to form a caprock, which in some places, rests upon older laterite (ferricrete) and silcrete profiles.

On the south-west margin of the shield, beneath the

Swan Coastal Plain, there is a widespread occurrence of siliceous and silicified rock which underlies meadow podzolic and "lateritic podsolic" soils (Pym 1955; McArthur & Bettenay 1960). The unit crops out in drainage channels near Mundijong (Fig. 7) where it is a syndepositional unit between upper and lower beds of the Guildford Formation. This silicified zone is correlated with the Karoonda Soil.

North of the Study Area in WA, the bronze coloured Wiluna Hardpan of Bettenay & Churchward (1974) occurs south of Mt Newman in the Pilbara area (Figs 2 & 11). The distinctive colour is due to the inclusion of "bronze" ferruginous nodules. There are two episodes of illuviation of clay separated by deposition of secondary silica. Upper horizons are not silicified and are probably younger. The hardpan consists of silica-cemented colluvium derived from profiles of "older laterite" and is part of a sequence of sediments and pedocretes – which from oldest to youngest – includes the Robe Pisolite, Wiluna Hardpan and calcrete.

Near Yeelirrie in the Eastern Goldfields, Glassford (1987) has described the Westonia Formation. The upper beds in the Westonia Formation contain fossilized wasp or beetle puparia that resemble beds unconformably overlying Parilla Sand in the Murray Basin later ferruginized and silicified in the Karoonda Soil.

On the south-east margin of the Australian Precambrian Shield the Karoonda Soil in the type section near Chowilla Homestead, in the Murray Basin, is a paleosol unconformably overlying the late Pliocene Parilla Sand. Here it occurs as thin layers of sand less than 0.5 m thick, including an horizon of fossilized wasp or beetle puparia, which has been ferruginized and silicified (Firman 1973). The soil takes its name from Karoonda, an important town in the Murray Basin (Fig. 3). Upstream from the type section it is represented by a silicified zone up to 2 m thick at the base of the Chowilla Sand where it separates the upper and lowermost beds of Blanchetown Clay (Gill 1973).

From the correlation of the magnetic polarity sequence with the absolute time scale (An *et al.* 1986), the age of the Karoonda Soil in the type section near Chowilla Homestead in the Murray Basin is Late Pliocene (in excess of 2.5 million years) and is older than the Olduvai event.

The Karoonda Soil has been identified at sea-level on the east coast of Eyre Peninsula, near Pidinga Lake north-west of Chundie Swamps on Eyre Peninsula, and at Wurdlata in the Great Australian Basin (Fig. 3).

Pleistocene – Recent sediments and soils

On the south-west margin of the shield, the sequence in the Perth Basin spans the time of recent changes in sea level, and records a series of Pleistocene-Holocene regressions and transgressions of the sea which have not yet been fully documented. Recent deposits cover all of the Perth Basin. They are usually less than 60 m thick and consist principally of shoreline and associated dune deposits with older fluvial beds underlying the Swan Coastal Plain, and colluvium in the piedmont zone.

The upper bed of Guildford Formation above the Karoonda Palaeosol contains a lateritic podzolic soil – which is virtually a laterite – with characteristic

ferruginous, mottled and pallid zones according to McArthur & Bettenay (1960). The writer believes that this part of the profile is equivalent to Menzies Formation in the Yeelirrie area. On the Swan Coastal Plain a late Cainozoic unit, the Bassendean Sand (Playford & Low 1972), overlies the upper bed of Guildford Formation and contains iron oxides called "coffee rock" (Mulcahy 1973).

In the Eastern Goldfields, the Menzies Formation (Glassford 1987) occurs along the axis of the Yeelirrie valley and along the floors and sides of tributary incisions. Red sandy clay and sandy claystone form the bulk of the formation. Lithologically, the basal beds resemble Hindmarsh Clay on the south-east margin of the Australian Precambrian Shield. Younger members of the unit contain calcrete which may indicate a stratigraphic position similar to that of the medial Pleistocene calcretes which overlie the Hindmarsh Clay on the south-east margin of the shield. The unit and its equivalents in other valleys on the shield have been drilled extensively in the search for uranium (Mann & Horwitz 1979).

Glassford & Semeniuk (1995) have presented evidence to suggest that the valley fill of major valleys in arid and semi-arid areas of the Yilgarn Craton is of aeolian origin. At Flinders Red Cliff at the head of Spencer Gulf in South Australia units showing aeolian cross-bedding overlies Hindmarsh Clay. Williams (1982) has suggested that they may be a few hundred thousand years old, and they may well be older.

On the south-east margin of the shield near Adelaide, Hindmarsh Clay occurs in the St Vincent Basin. Lindsay (1969) has correlated the basal beds of Hindmarsh Clay, which contains a fauna with a definite marine influence (possibly uppermost Pliocene transitional to Pleistocene) with Carisbrooke Sand. At Hallett Cove in the same area, Hindmarsh Clay equivalent with a well-developed zone of ferruginous mottling about 2 m above the base of the lowermost unit contains the Brunhes/Matuyama boundary (0.70 Ma) according to Pillans & Bourman (1996),

A mottled zone resembling the Ardrossan Palaeosol overlies the lowermost unit.

A younger silcrete of Pleistocene age has been developed in the Pliocene-Pleistocene Hindmarsh Clay and equivalents of the Mt Lofty Ranges at Baldoon Homestead near Sedan, in piedmont clays near Port Lincoln (where the local name is Boston Bay Silcrete Firman 1967a), at Ceduna (Thevenard) on Eyre Peninsula and interbedded with Pleistocene Mount Willoughby Limestone inland near Coober Pedy. These silcretes resemble siliceous lenses exposed on the eroded top of silty sand in the Murray River near Mundijong in Western Australia.

In the Murray Basin of South Australia, bedded gypsum deposits occur in the upper beds of Blanchetown Clay. Calcareous loess appears below the uppermost lacustrine limestone (Bungunnia Limestone) and underlies the Ripon Calcrete and Bakara Calcrete, which in this area represent the Medial Pleistocene Bridgewater Formation of the coastal margin (Wetherby 1975; Firman 1982; Pillans & Bourman 2001).

Summary and conclusions

Geological events controlling the development of weathering zones, pedocretes and palaeosols along the south-west margin of the Australian Precambrian Shield were as follows:

1. Darling Fault zone reactivated. Marine sediments of the Proterozoic Cardup Group displaced, possibly during the early Palaeozoic, so that they now lie over 15 km below younger sediments west of the Darling Fault.

2. Rifting and development of the graben continued. Palaeozoic sedimentation began during the opening of the Dandaragan Trough. Deep valleys were incised along the basement margin.

3. Deep weathering of post-Ordovician/pre-Permian time created the Playfair Weathering Zone. Strong ferruginous mottling.

4. Carboniferous-Permian continental sedimentation extended onto the Yilgarn Craton. Glaciation preceded deposition of coal beds. Permian palaeochannels were incised into the Playfair Weathering Zone.

5. Sedimentation continued into the Triassic. No major movements of faults occurred on the eastern margins of the areas now identified as the Dandaragan and Blackwood plateaux after the Jurassic.

6. An early Cretaceous high-sea eroded the Darling Scarp and the Ridge Hill Sandstone was deposited.

7. Separation of Greater India at the end of the early Cretaceous. Renewed faulting. There was a wide marine gulf in the Cretaceous. Cretaceous sediments are now found at the same level on either side of the Darling Fault.

8. A pallid zone (Arckaringa Weathering Zone) developed at the top of the Playfair Weathering Zone on the shield and in Cretaceous sediments to the west. A ferruginous mottled zone (San Marino mottled zone) was emplaced below an ancient erosion surface cut across the bleached zone.

9. Mesozoic – early Cainozoic separation of Gondwana. Revival of downwarping around the south-west margins of the Australian Precambrian Shield. Palaeocene-Eocene dissection. Eocene sedimentation.

10. Middle Eocene high sea. Groundwater table rises. Retreat of the high sea and formation of the Darling Range Bauxite above the Playfair Weathering Zone and Arckaringa Weathering Zone from reconstituted colluvium.

11. Eocene-Miocene Greenmount Ferricrete (Yallunda Ferricrete equivalent) formed above older weathered zones. Ferricrete includes pisolites accumulated during repeated local reworking of granular material.

12. Gravels and sands deposited east of the Darling Fault were silicified to form the Miocene Calingiri Silcrete. Retreat of the Miocene sea.

13. Uplift of Tertiary basin sediments. Erosion of older ferricrete.

14. Jumperdine Ferricrete developed as a cap over conglomeratic sediments and older sediments forming part of the "laterite bench".

15. The "laterite bench" was displaced down to the west of the Gingin, Darling and Whicher Scarps. Erosion of the Arrowsmith and Gingin areas and incision of streams through the high-level laterite and the Ridge Hill Shelf continued.

16. A rise of the Late Pliocene sea led to deposition of Yoganup Formation against the scarps. Retreat of the Late Pliocene sea was followed by erosion of the Dandaragan and Whicher Scarps.

17. Deposition of Late Pliocene-Pleistocene clays and sands on the Swan Coastal Plain.

18. Formation of the Karoonda Soil.

19. Deposition of clays and sands continued.

20. Development of "lateritic podsolic" soil in upper beds of Guildford Formation.

21. Calcrete pans formed in older brown soils.

The stratigraphic relationships of the weathering zones, pedocretes and palaeosols are shown on Figures 5 & 6.

In previous discussions of palaeosols in ancient soil profiles (Firman 1968; Firman & Lindsay 1976; Firman 1988; Firman 1994), palaeosols were described in the context of the geological evolution of materials on the south-east margin of the Australian Precambrian Shield: The conclusions from those studies were that pedogenic events were episodic; that is, weathering zones, pedocretes and horizons in palaeosols were formed in different ways at different times, due mainly to changes in climate and groundwater composition. "Laterite" and silcrete profiles were shown to be assemblages of weathered rock, sediments and palaeosols, the assemblages being characteristic of different morpholithological provinces.

The study of weathering zones, pedocretes and palaeosols on the south-west margin of the Australian Precambrian Shield has confirmed the earlier conclusions derived from South Australia (Fig. 6): sedimentary sequences (some of which are greater than a group or supergroup) are intercalated in the profiles between the Playfair Weathering Zone and the Arckaringa Weathering Zone, between the San Marino mottled zone equivalent and the Greenmount Ferricrete, which is itself a mixed sediment cemented by iron oxides, and (after erosion of the ferricrete and formation of the Calingiri Silcrete) between the Playfair Weathering Zone and the younger Jumperdine Ferricrete. Sediments also are intercalated between the Jumperdine Ferricrete and the Karoonda Palaeosol.

The oldest weathering zones mark bounding surfaces that extended to other continents prior to the break up of Gondwana. The ferricretes and silcretes mark surfaces developed in southern basins during the separation of Australia and Antarctica. Older structured clays mark soil development along the piedmont zones marginal to mountain chains in the Pliocene, and calcretes identify older brown soils developed during sea-level changes in the medial Pleistocene.

Younger surfaces are recorded by palaeosols formed within the great soil groups which themselves are soil assemblages with a world-wide distribution (Firman 1986, 1988, 1994).

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Ken joined the Royal Society of Western Australia Council in 1985/86, serving for some 10 years. He was President in 1991/92. In 2006, Ken also was awarded the prestigious Australian Academy of Science *Mawson Medal*.

Ken McNamara's research has concentrated on using the fossil record to unravel the patterns and processes of evolution. The main focus has been on interpreting the patterns of evolution in terms of heterochrony – variations to the timing and rate of organisms' development. In addition to writing many papers on heterochrony he has co-authored the main textbook, written a popular book and edited two other books on the subject.

Star-Crossed Stones – the archaeology, mythology and folklore of fossil echinoids (Medal Address July 2005)

In his seminal book *Micrographia*, published in 1665, the great English physicist, astronomer, geologist, chemist, architect and microscopist Robert Hooke remarked that fossils 'do owe their formation and figuration, not to any kind of *Plastick virtue* inherent in the earth, but to the Shells of certain Shell-fishes which...came to be.... fill'd with some kind of Mudd or Clay or *petrifying* Water, or some other substance, which in tract of time has been settled together and hardned (sic) in those shelly moulds into those shaped substances we now find them.' Like one or two other free thinkers on continental Europe, Hooke had come to realise that fossils were the remains of once living organisms. While this may be of no surprise to us today, in 17th century Europe such thoughts were not only radical, but verged on the heretical. Foremost in Hooke's interpretation were little fossils that he had collected as a boy on the Isle of Wight in southern England and which he called 'button-stones' and 'helmet-stones'. The former are what we now know as regular echinoids (sea urchins), the latter are another kind of echinoid called a heart urchin (see Fig. 1). Both occur commonly as fossils in Cretaceous and Jurassic rocks in England, through much of Europe and the eastern Mediterranean region.

While fossil echinoids subsequently played a significant early role in supporting Darwin's theory of

Figure 1. A 'shepherd's crown' the echinoid *Micraster* collected by Mr A. Smith from a field in Linkenholt, Hampshire.

evolution, for thousands of years earlier they had been the fossil that had most attracted the attention of humans. The presence of fossil echinoids in many archaeological deposits indicates that people have been collecting them for literally hundreds of thousands of years. By analysing the archaeological context in which fossil echinoids are found and also the folklore that has been attached to them, and which has survived into recent times, it is possible to reconstruct some of the myths that might have been associated with these star-crossed stones. Information from archaeology derives from two sources. One is from artificial alteration of the fossil itself, or of the rock on which it occurs. The second is from the archaeological association of the fossil, in other words where it was found and with what. For instance, many examples are known of fossil echinoids having been buried with human remains. There is evidence from many archaeological sites throughout much of Europe, the Near East and northern Africa, that these fossils attained the status of cult objects, imbued with powerful spiritual significance. These magical powers have, over thousands of years, dwindled into the folklore that even well into the last century, saw them regarded as either apotropaic objects (capable of warding off evil) or objects that bestowed luck on their finders.

The earliest evidence for someone specifically collecting a fossil echinoid is from an Acheulian hand axe crafted about 400,000 years ago and found in southern England at Swanscombe, Kent. Embossed on this hand axe is the fossil echinoid *Conulus*, preserved as a distinctive five-rayed star (Fig. 2). The collector of this flint, probably a member of *Homo heidlebergensis*, only worked one side of the axe. Had they worked the other side much of the fossil would have been destroyed. This points to the fossil having been collected and incorporated into a tool because of its aesthetic appeal, probably its five-rayed star pattern. Other Early Palaeolithic flint axes are known from France that similarly have fossil echinoids incorporated into them. Although we can only conjecture, it is possible that the

fossil may have been thought to have imbued the axe with special powers. *Homo neanderthalensis* also appears to have taken a liking to fossil echinoids, distinctive Mousterian style scrapers having been found in France, some made entirely from the fossil, others incorporating them into the body of the tool. This tradition was continued in *Homo sapiens*. In recent years a large number of Neolithic flint tools have been found in Belgium that incorporated fossil echinoids.

It was during Neolithic times, after many societies had given up their nomadic hunter-gatherer existence and established permanent settlements, that we first find evidence of fossil echinoids being used as grave goods. In most cases where they have been found in this context, they are either the sole or dominant grave good. Often a single fossil was placed in a grave with the body. However, examples of large barrows (burial mounds) are known from Brittany that upon excavation have been found to contain nothing but a single fossil echinoid – not even a body. This signifies the attachment of a high spiritual significance to these fossils in northern Europe during Neolithic times.

Burial of fossil echinoids with bodies became quite extreme on occasions. In one Bronze Age grave near Dunstable in England the remains of a young woman and child were found with more than 300 fossil echinoids buried with them (Fig. 3). The most extreme example, though, was a Bronze Age site near Héricourt in France, where a tomb was uncovered that contained a single human skull, a cup made from a deer's horn and what

Figure 2. Acheulian hand axe, about 400,000 years old, from Swanscombe, Kent containing the echinoid *Conulus*.
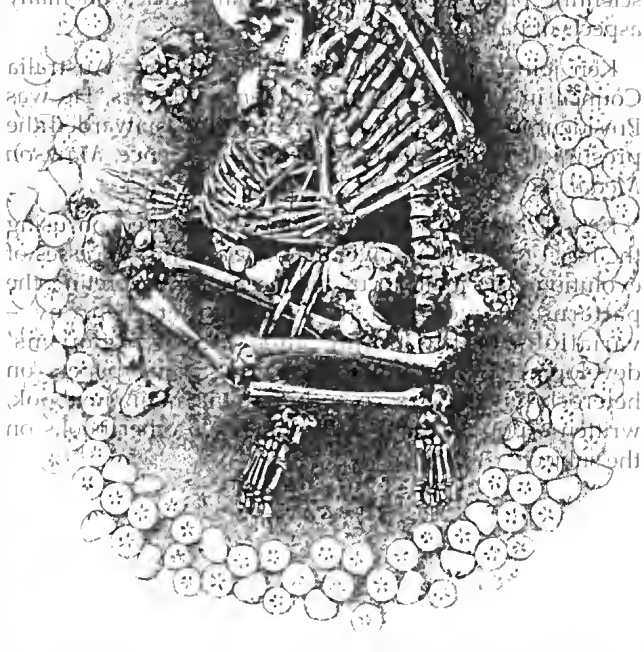

Figure 3. Drawing by Worthington G. Smith of skeleton of woman and child in grave with more than 300 fossil echinoids that he excavated near Dunstable is 1887.

was estimated to be 2 to 3 cubic metres of fossil echinoids. It has been calculated that this could represent up to 30,000 fossils.

The discovery of a fossil echinoid with a stone axe in a pot in an Iron Age cremation deposit in Kent in southern England, indicates a link with Norse mythology through the god Thor. Folklore gathered in Denmark and southern England in the early 20th century indicates that both fossil echinoids and stone axes were called 'thunderstones'. These were thought to have been thrown to Earth by Thor. This god was not only a thunder god, but also the peasant's god who protected them. Thus these fossils were placed near windows and doors not only to ward off lightening strikes, but also to protect the house from evil. Other folk names given to fossil echinoids in England include 'shepherd's crowns' and 'fairy loaves'. Both of these names are likely to have derived from Celtic or pre-Celtic terms and beliefs in the association of these object with the afterlife. Their frequent occurrence in burial mounds (sites of passage from this life to the next), points to a significance attached to the fossils associated with ensuring the rebirth of their bearer. These spiritual beliefs degenerated in Christian times into folk traditions of 'good luck' associated with the fossils, such that 'fairy loaves' were thought to help keep the milk fresh and ensure that the bread would rise.

Fossil echinoids appear to also have been significant in the Mediterranean region from at least as far back as the Neolithic. However, they are only rarely found associated with burials. They seem to have had a more practical use, for many had holes drilled through them so they could be used a spindle whorls. However, even here the use of objects with the five-rayed star pattern suggests their use may also have had some degree of spiritual significance. A drilled fossil from one of the earliest Neolithic settlements in the eastern Mediterranean, 'Ain Ghazal in Jordan, may well have been used as a fertility object, due to the location of the hole (see Fig. 4). Other fossils from Neolithic and Iron Age sites in Jordan have been altered to enhance the five-rayed pattern. It is possible that this was seen to be representative of the human form, akin, in Renaissance times, to Leonardo da Vinci's Vitruvian Man.

One of the most spectacular fossil echinoids is one found at Heliopolis in Egypt. Hieroglyphs were inscribed on this fossil in about 1500 BC informing us of the name of the priest who found it and where he found it – the quarry of Sopdu, a god sometimes known as the 'Morning Star'. The presence of a distinct five-rayed star

Figure 4. Fossil echinoid *Coenholectypus* with drill hole, from Neolithic site, 'Ain Gazal, Jordan. Possibly used as a fertility symbol, the five-rayed pattern perhaps seen as representative of the human form.

on this fossil, and the extensive use of this symbol by ancient Egyptians in their burial chambers to symbolise the stars in the sky to which the spirit of the pharaoh returned, suggests that these fossils might have played an important role in Egyptian funeral rites.

The apotropaic powers that fossil echinoids are thought have possessed shows a close parallel with the same attributes of the five-rayed star symbol on its own. This symbol was in use as far back as nearly 5,000 years ago in Mesopotamia. The mediaeval knight Sir Gawain had one on his shield because it symbolised chivalry, courtesy, piety and kindness. It was used commonly in mediaeval times above doors of houses or stables, or on cots, to keep the devil at bay. Perhaps emulating this belief, the presence of fossil echinoids placed around windows on a mediaeval church in Hampshire in southern England might be thought to have functioned in a similar way. Given the very long fascination that humans have had with fossil echinoids, it is not unreasonable, I believe, to consider that the five-rayed star, that today is one of the most ubiquitous of all symbols, had its origins in people's captivation by these star-crossed stones.

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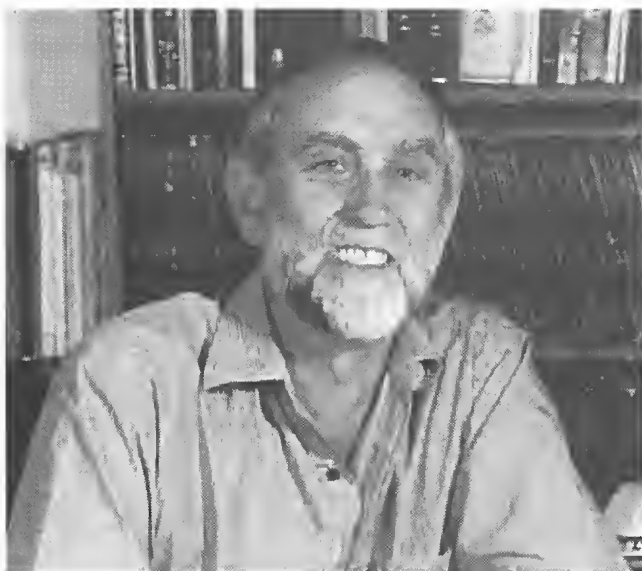
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Born in Brighton, England in 1942, David Groves was educated at Varndean Grammar School before emigrating to Tasmania and attending Hobart High School. He gained a First Class BSc Honours from the University of Tasmania in 1963 and a Ph.D. from that university in 1968. He spent the remainder of his time employed with the Geological Survey of Tasmania, mainly mapping on the west and northeast coasts of the island. Among many other technical papers, he published Bulletins on the famous Mount Bischoff tin field and on the Blue Tier Batholith of north eastern Tasmania.

David joined the University of Western Australia (UWA) in 1971 as a lecturer in economic geology. During his early years at UWA, he taught economic geology, ore genesis, structural geology and field mapping at all undergraduate levels. His research was mainly on evolution of the Archaean Yilgarn and Pilbara Blocks and the origin of komatiite-associated nickel deposits. David progressed from Lecturer to Senior Lecturer to Associate Professor, and by 1987 was a Professor and Director of the Key Centre for Strategic Mineral Deposits. By that time, his main research interests had evolved to the genesis of gold deposits and the use of GIS in conceptual exploration targeting. David remained as Director of the Centres for Strategic Mineral Deposits and its successor, the Centre for Global Metallogeny, until his early retirement in 2005 to facilitate the generation of a new

centre, the Centre for Exploration Targeting, at UWA. In the last few years at UWA, his interests have focused on global metallogeny, the influence of lithosphere on the temporal and spatial distribution of mineral deposits, and conceptual exploration. In 2006, he became Emeritus Professor at UWA as well as a company director and industry consultant.

Throughout has academic career, David authored or co-authored over 500 published papers and supervised over 80 PhD, 35 MSc and 120 BSc Honours students. His major contribution has been to mentor young geologists who have gone on to very successful careers in industry or academia.

During his career, David has been both President of the Geological Society of Australia and its WA Division and President of the Society of Economic Geologists, and is now President Elect of SGA (the European Society of Economic Geologists). He has also served on a number of national and international committees. Honours received include the Stillwell Award of the Geological Society of Australia (GSA), the Clarke Medal of the Royal Society of New South Wales, the inaugural Gibb-Maitland Award of the W.A. Division of GSWA, the Silver Medal of the Society of Economic Geologists, the Geological Association of Canada Medal, the Jubilee Medal of the Geological Society of South Africa, the Goldfields Medal and the Kelvin Medal of the Royal Society of Western Australia. David became a Fellow of the Australian Academy of Science in 2005.

Controls on the Temporal Distribution of Ore Deposits: An Explanation for the Mineral Wealth of WA (Medal Address, November 2005)

Mineral deposits exhibit heterogeneous distributions, with each major deposit type showing distinctive, commonly unique, temporal patterns. These reflect a complex interplay between formational and preservational forces that, in turn, largely reflect changes in tectonic processes and environmental conditions in an evolving Earth. Sedimentary mineral deposits mined for redox sensitive metals show highly anomalous temporal patterns in which specific deposit types are restricted to particular times in Earth history. In particular, palaeoplacer uranium, banded iron formation (BIF) and BIF-associated manganese carbonates that formed in the early Precambrian do not reappear in younger basins. The most obvious driver is progressive oxidation of the atmosphere, with consequent long-term changes in the hydrosphere and biosphere, the latter influencing the temporal distribution and peak development of deposits such as Mississippi Valley types (MVT), hosted in biogenic sedimentary rocks.

In terms of tectonic processes, the major drivers were the supercontinent cycle and evolution from plume-dominated to modern-style plate tectonics in a cooling Earth. Consequent decrease in the growth rate of continental crust, and change from thick, buoyant sub-continental lithospheric mantle (SCLM) in the Precambrian to thinner, negatively buoyant SCLM in the Phanerozoic (Fig. 1), led to progressive decoupling of formational and preservational processes through time. This affected the temporal patterns of deposit types including orogenic gold, porphyry and epithermal deposits, volcanic hosted massive sulphide (VHMS), palaeoplacer Au, iron oxide, copper gold (IOCG), platinum group elements (PGE), diamond and probably massive sulphide SEDEX deposits.

As Western Australia is dominated by Archaean cratons and intervening Proterozoic belts, it is largely underlain by thick buoyant SCLM. This largely protected the gold and nickel deposits, in Archaean cratons from erosion, enhancing the mineral wealth of Western Australia. The great stability of the SCLM also aided in the generation of surficial bauxite and laterite nickel deposits during the prolonged tropical to arid weathering cycles that affected the State.
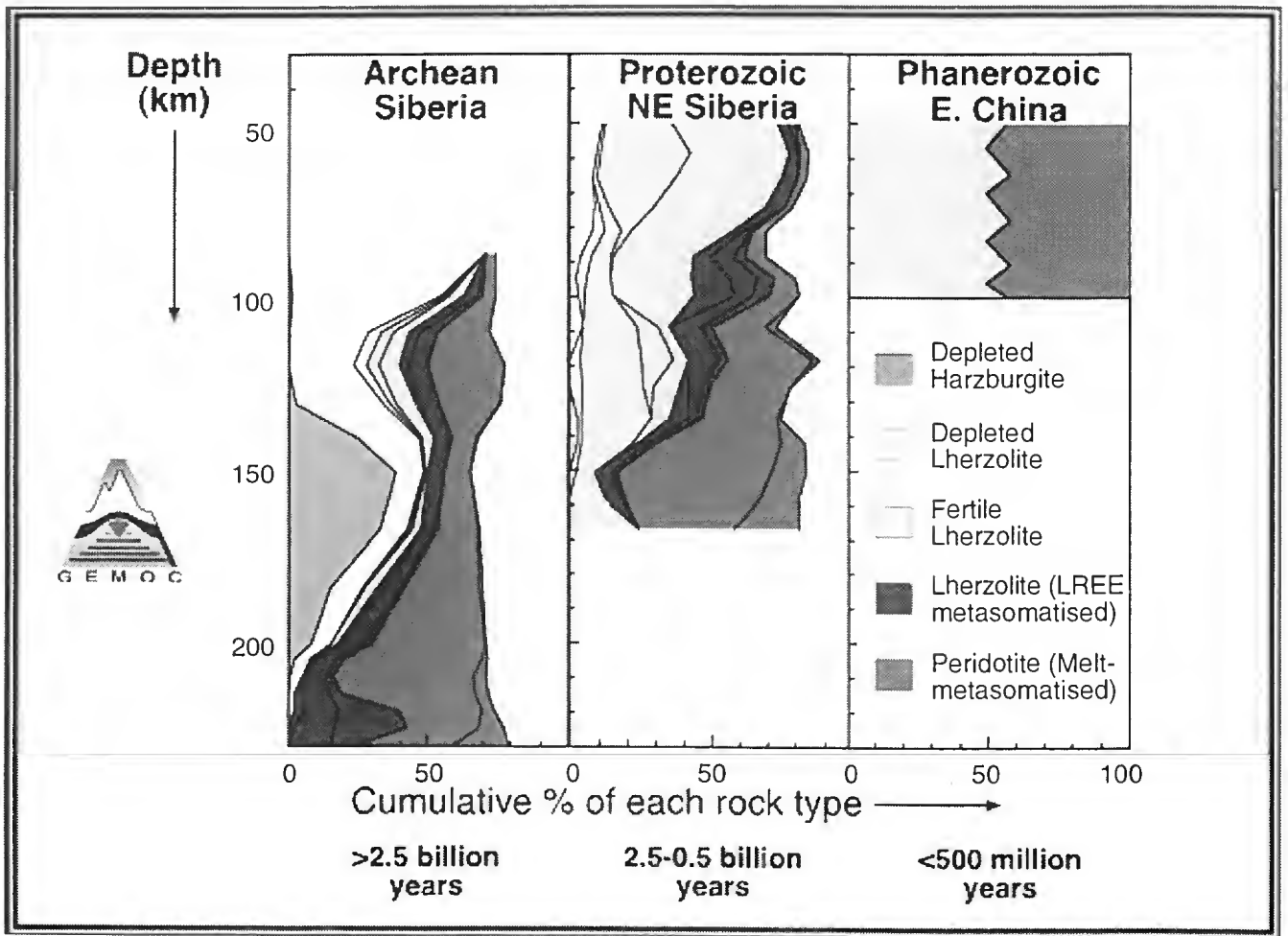
Figure 1. Depth and depth variation in composition of selected Archaean, Proterozoic and Phanerozoic lithospheric sections, showing changes in both depth and composition of sub-continental mantle lithosphere with time. Mean densities (at 20 °C) and relative buoyancy also shown. Modified from GEMOC.

Occurrence of the Barking Gecko *Underwoodisaurus milii* (Bory 1825) (Gekkonidae) in the Pilbara Region, Western Australia

Notes on ....

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Abstract. To date, a total of five specimens of *Underwoodisaurus milii* have been collected from the Pilbara Region of Western Australia and lodged at the Western Australian Museum, along with observational records of two other individuals. These records from the Pilbara represent a significant range extension for the species, to the north and east of that currently known for Western Australia.

Keywords: *Underwoodisaurus milii*, Barking Gecko, Thick-tailed Gecko, Pilbara.

Introduction

The Barking Gecko *Underwoodisaurus milii* (Bory 1825) is a species known to occupy a number of habitats, including woodlands, shrublands, rock outcrops (Storr *et al.* 1990; Wilson & Swan 2003) and under rubbish (Bush *et al.* 1995), emerging to forage at night (Cogger 2000). Currently the accepted range of this species extends across a large part of the southern half of Australia, from Rockhampton, Queensland to Shark Bay, Western Australia (Storr *et al.* 1990; Wilson & Swan 2003).

Methods

Incidental captures of *U. milii* were made during two separate opportunistic vertebrate fauna surveys in the Pilbara Region of Western Australia. Surveys were conducted by *ecologia* Environment Pty Ltd at West Angelas mining lease and at Packsaddle Range. Specimens collected were lodged with the Western Australian Museum (WAM). The individuals captured from Packsaddle Range were located whilst head-torching. Locations of all specimens of *U. milii* lodged with the WAM, as well as some observational records are shown in Figure 1.

Results

A single specimen of *U. milii* was collected on the 14th of June 1997 at West Angelas (WAM R129895). This
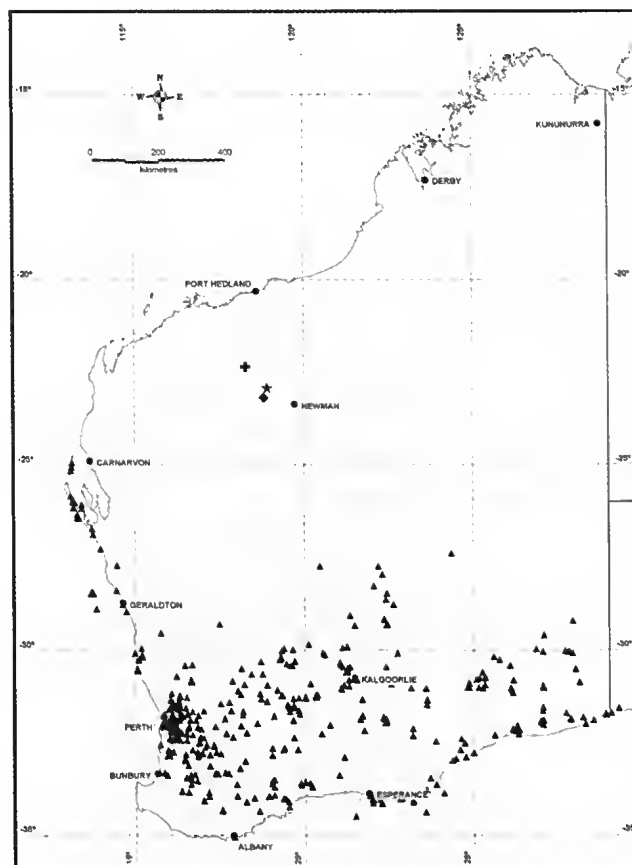
Figure 1. Map showing locations for all specimens of *U. milii* lodged with the WAM, along with locations of some observational records. ▲ denotes specimens lodged with the WAM. ✚ denotes Michael Kearney's record. ★ denotes *ecologia* Environment records from Packsaddle Range. ◆ denotes *ecologia* Environment record from West Angelas.

individual was captured in a rocky gully with *Triodia* spp. hummocks and fallen boulders at the base and on the slopes (*ecologia* Environmental Consultants 1998).

A further four specimens of *U. milii* (Plate 1) were collected from Packsaddle Range on the night of the 7th of May 2004 (WAM R157513, R157520, R157522 and R157525). Three were captured on and around a graded track running through a major gully, with piles of broken
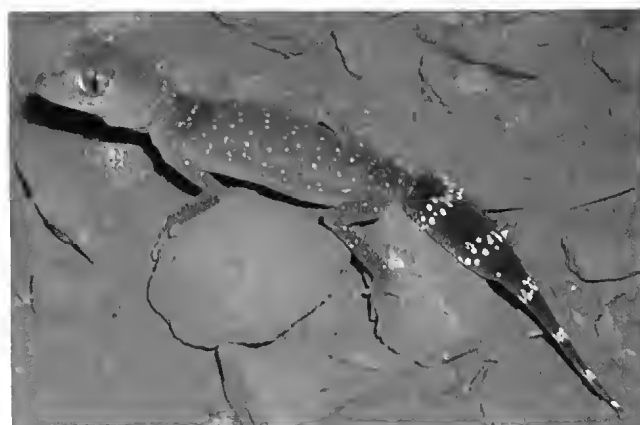
Plate 1. *Underwoodisaurus milii* at Packsaddle Range, Western Australia. The habitat on which this species was recorded can be seen in the photograph. Photograph: M. H. M. Menz.

rock pieces along the sides. The first individual was found away from the road, on a slope under a slab of rock and the other three were found crossing the track. Another individual was captured from the same location that night, but was released.

Another individual of *U. milii* was observed near Handrail Pool, Karijini National Park in May 2005 (M. Kearney Personal Communication).

Discussion

The individuals collected from Packsaddle range appear to be more gracile in morphology than individuals from the south-west. The overall colouration also appears to differ slightly, though this may be due to individual variation.

These records of *U. milii* in the Pilbara Region of Western Australia represent a significant extension to the known range of this species (Figure 1). Previously known to occur only as far as slightly north of Shark Bay (Storr *et al.* 1990; Wilson & Swan 2003), these individuals extend the range further north and east of the known distribution in Western Australia. It is not yet known whether this is a continuous extension to the range of this species, or whether this represents a disjunct population. Strong & Gillam (1983) recorded the first specimen of *U. milii* for the Northern Territory from the stomach of a feral cat and Cogger (2000) mentions a population in central Australia, which is also shown on the distribution map in Wilson & Swan (2003). Though it is difficult to infer the possible wider occurrence of this species in the arid zone, these records from the Pilbara along with those from central Australia and the record from the Northern Territory may indicate that the species is colonising the arid zone, or more likely, surviving in relict populations. Potentially isolated populations such

as this need to be considered in terms of their conservation significance, with regard being given to the degree of structuring of genetic divergence. Questions such as this need to be quantified with the use of targeted molecular studies. The results from Mitochondrial DNA analysis on tissue from one of the individuals from Packsaddle Range indicates that it is not a separate species from specimens examined from Perth, the Goldfields or the Shark Bay region (S. Donnellan Personal Communication).

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Honorary Editor's Preface

This year, on February 15th, Dr John Beard, former Director of the Kings Park Botanical Gardens, and former President of our Royal Society of Western Australia, celebrated his 90th birthday. The Council of the Royal Society of Western Australia, in recognition of his contribution to science over 60 years, decided to dedicate this issue to him as a celebration of his life in Botany. A short history of John's professional life has been written by Dr Kingsley Dixon, and included here also is an extensive bibliography of John's publications that enables readers to explore his work

The contribution Dr Beard has made to botanical and vegetation science in Western Australia has been extensive: from the design, logistics and management of the botanical gardens at the Kings Park Botanical Gardens, to documenting the vegetation of Western Australia, to undertaking regional mapping and producing the first regional vegetation maps in the State.

The history of the professional life of Dr John Beard makes interesting reading, and outlines a career that spans numerous terrains from Trinidad to South Africa, to Botanical Gardens at Kings Park and at Sydney, to all corners of Western Australia while mapping the vegetation complexes of the State.

As an issue dedicated to John Beard's work in plant science, Volume 89(3) also includes papers from a variety of plant science research currently being undertaken in Western Australia: from pollination in *Eucalyptus marginata*, diatoms as biomonitors of mine-lakes, the fern *Asplenium aethiopicum* recolonising karri forest following timber harvesting and burning, traditional taxonomy in a description of *Synaphea xela* a new Proteaceae from Western Australia, to the use of pollen in reconstructing Holocene vegetation history on a beachridge plain.

Dr Kathy Meney
Honorary Editor
Royal Society of Western Australia

Celebration of a Life in Botany

Dr John Stanley Beard – on the occasion of his 90th Birthday

John Beard was born on February 15th 1916 at Gerrards Cross, a dormitory suburb on the west side of London. Initially studying architecture at University College, London, to follow in his father's footsteps, John later changed to the School of Forestry at Oxford. After graduating in 1937, he applied to the Colonial Office for an appointment as a colonial forest officer, and was sent to Trinidad in the West Indies as Assistant Conservator of Forests. In 1940, John returned to Oxford for a postgraduate course which was customary in the Colonial Service. There, the late Dr Burtt Davy kindled his interest in forest ecology, suggesting work in Trinidad as the basis for higher degrees.

Following his marriage to Pamela Davey in England in 1940, John returned to Trinidad as Research Officer to the Forest Department, with the task of using aerial photographs to prepare land-use maps of the alienated land and vegetation maps of the Crown Land. He was able to use this work as a basis for his theses on the natural vegetation of Trinidad and Tobago. These were submitted first for his BSc at Oxford, and later for his doctorate which was conferred in 1945 (this work was published as Oxford Forestry Memoir No 20 in 1946). In 1943, John was seconded to the Colonial Development and Welfare Organisation for work in the adjoining Windward and Leeward Islands and Barbados where he was to advise the 10 governments concerned on the foundation of forest services. He wrote reports and forest laws, recruited staff, endeavoured to secure forest reservation, made land-use and vegetation maps, compiled a herbarium of trees and shrubs, and conducted surveys of forest resources. Later, this led in 1949 to the publication of *The Natural Vegetation of the Windward and Leeward Islands*. Three months leave in Venezuela in 1945 included an expedition to the Guiana Plateau to study the savanna vegetation. John's work on vegetation in the American tropics culminated in the drafting of a physiognomic system of classification of climax communities. While now outdated, this work was considered classic for a time and was outlined in textbooks, *e.g.*, Cain and Castro's *Manual of Vegetation Analysis* 1959, and P W Richards' *The Tropical Rainforest* 1952.

After the war, John secured an appointment in South Africa as silviculturist with the Natal Tanning Extract Company working on crop improvement in the wattle industry. The company had 100,000 acres of plantations in Natal and the Eastern Transvaal, as well as associated enterprises in Rhodesia, Tanzania, Kenya and Morocco which were visited from time to time. As a hobby, assisted by grants from the South African CSIR, John took up the study of the genus *Protea*. Much later he was able to publish *The Proteas of Tropical Africa* illustrated by Lura Ripley, a South African botanical artist. John also developed an interest in the botanic gardens of Pietermaritzburg, which had been established by the

Botanic Society of Natal in 1874. John became President of the Society in 1955, and became directly responsible for the Gardens which at that time were in a moribund condition and starved of funds. The interests aroused by this honorary work led him to apply for the post of Director for the as yet to be established botanic garden at Kings Park, Perth, taking up the position in September 1961.

The new Garden at Kings Park was to specialize in the study, cultivation, and display of Western Australian native plants. However, there were problems in establishing the Garden, as there was a lack of basic information about native plants, *e.g.*, edaphic issues associated with the specialized habitats in which many of the most beautiful species grew. There was also a lack of basic information about native plants – how many species existed in Western Australia, and their phytogeography. Additionally, there were difficulties

In academic dress for "Final Schools" at Oxford University in 1937.

Addressing a field day for wattle growers, Natal, South Africa, in the 1950s.

procuring suitably experienced local staff, as at that time there was no formal training in horticulture in Western Australia (later there were to be evening classes at Kings Park, until the coursework was taken up by the Education Department), so the first gardeners and nurserymen were horticulturists from overseas institutions. Also, to ensure the best possible opportunity for establishing the botanic garden along international principles, the Park Superintendent, Arthur Fairall, was recruited from his post as Director of Parks in

Talking to the Honourable David Brand and his wife after the official opening of the Kings Park Botanic Garden in October 4th 1965.

Pietermaritzburg. The first Nurseryman was Ernst Wittwer, a Swiss who had also trained at Kew Gardens. An Australian, Fred Lullfitz, who had been operating a wildflower nursery at Cannington, filled the post of Seed Collector, making many important collecting trips between processing the seed for the nursery. A nursery was established during the first year (1962), with six hundred seed lots sown; the first plantings in the Botanic Garden were made in 1963. The Botanic Garden was officially opened in 1965.

However, the lack of basic information on native flora continued to be a problem. In order to advance Western Australian botanical science, John initiated an inventory of plant species and an inventory of plant communities (vegetation types). A list of plant species classified into genera and families had been drawn up some years before by the then Government Botanist, Charles Gardner, but this provided names only. "The Beard catalogue", as it became popularly known, indicated for each species what kind of plant it was, height, flower colour, flowering time and what district in the State it was found – in other words, the basic information needed by the horticulturist. Published by the Society for Growing Australian Plants in Sydney in 1965, it remained a 'best seller' for many years.

The task of cataloguing of plant communities (*i.e.*, vegetation mapping) was difficult and required considerable effort, in fact 17 years, but it must be remembered that in the 1960s even publication of basic topographic maps had barely commenced, and although aerial photography was available, access tracks into remote areas were still in the progress of being made.

An attempt to reach an oil camp in the Great Sandy Desert , in the 1970s, after freak rains.

The vegetation mapping necessitated field work to record plant species, soil associations and vegetation types, codifying this information and translating it onto aerial photographs to be later transferred to 1:250,000 topographic maps. Fieldwork for this project started in 1963, initially carried out by John accompanying Fred Lullfitz on his seed-collecting expeditions. As the publication stage approached, political problems were unfortunately encountered. This was the period of almost unlimited farming expansion in the wheatbelt and the government did not wish prior knowledge of vegetation to be broadcast in case there was popular demand for conservation reserves. After nine years as Director of Kings Park, this impasse led John to take up the Directorship of the Royal Botanic Gardens in Sydney in late 1970. During his time at Kings Park, in addition to botanical work, there was design and construction of the spiral tower (now known as the 'DNA Tower'), construction of the lake at the bottom end of the park (Western Power Parkland) and of the longwalk or vista joining the two.

John retired in 1973 from the Directorship at Sydney, and on returning to Perth continued on with the task of completing the vegetation maps of Western Australia. On his return to Perth, there also was a fortunate meeting with Professor Martin Webb who had newly arrived as head of the Geography Department at the University of W.A., and shared an interest with John in promoting vegetation mapping. The two collaborated in producing the Vegetation Survey of Western Australia. Two map series were undertaken: one at a scale of 1,000,000 with seven sheets in colour covering the whole State,

published by the University of Western Australia Press with support from the ABRS, and the other with 24 sheets at 1:250,000 covering the southwest only where there would be interest in more detail available at the larger scale. These maps could only be printed in black and white and were published initially by the University Geography Department. Maps were accompanied by an explanatory booklet. Fieldwork was aided by the generosity of Dr Jack Sunderman, who loaned John his personal Land Rover and caravan.

The Vegetation Survey was completed in 1981 in time for a map display at the International Botanical Congress in Sydney. To produce the maps, it is estimated to have involved road traverses totaling some 150,000 km, recorded in 1100 pages of longhand notes. Some 6870 botanical specimens were collected and about 1000 photographs taken. The area mapped amounts to the western third of Australia, about 2,500,000 square kilometres and must be a record for an area mapped in this way by one person. Subsequently, John continued to be active in ways that satiated his botanical interests. A single vegetation map of the State at 1:3,000,000 was produced by the Forests Department, and one at 1:10,000,000 was included in the sesquicentary publication *An Atlas of Human Endeavour.* John himself published a book *Plant Life of Western Australia* in 1990 to illustrate some 500 of the photographs taken on fieldwork.

In 1983, John was awarded the Royal Society of Western Australia medal "for distinguished work in science", and later became President of the Society for the year 1986–87. John continued publication of scientific papers. The last botanical paper, *Species richness and endemism in the West Australian flora,* written in conjunction with A R Chapman and P Gioia, from the Western Australian Herbarium, was published in 2000. Interested in geomorphology, John investigated the evolution of drainage systems in successive parts of the State, with papers in 1998, 1999, 2000, 2003 and 2005. The latest publication is in press. This continued an earlier interest in palaeodrainage, a map and booklet having been published in 1973. In 2003 John was appointed a Member of the Order of Australia (AM) in recognition of his services to science.

A bibliography of Dr John Beard's work is included herein.

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Low success of controlled pollination in *Eucalytpus marginata* (jarrah)

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Abstract

The success of controlled pollination techniques was investigated for clones and wild trees of *Eucalyptus marginata*. The number of pollen tubes in the style was used as a measure of pollination success. The stigma was receptive from 3–11 days after anthesis, but it appeared that stigmatic receptivity may be highest from 4–7 days after anthesis. Flowers were isolated using aluminium foil squares, and fresh pollen was found to be more effective for pollination success than processed pollen. Results were inconclusive comparing self- to cross-pollination success, and no difference was found comparing pollination success in clones and wild trees. However clones generally tended to flower earlier than the wild trees, whatever their origins, and very few mature fruits resulted from any controlled pollinations in jarrah clones. Clones also produced a lower proportion of mature capsules from the flowers produced (Wheeler 2004)

Keywords: pollination, *Eucalyptus marginata*, stigma, style

Introduction

Control-pollination techniques have been developed in several species of *Eucalyptus* as a tool to assist in selective breeding. Controlled pollination has been used to improve seed yield (Harbard *et al.* 1999; Moncur 1995), control the level of outcrossing in seed orchards and improve breeding through knowledge of fertility and compatibility, achieve interspecific hybridisation, and study self-incompatibility levels in *Eucalyptus* species. Detailed knowledge of the pollination biology of *Eucalyptus marginata* (jarrah) is essential to design an effective seed orchard, or to conduct controlled pollination for genetic improvement of trees. This study was undertaken to assist in the development of control-pollination techniques in *E. marginata*, which could be used for the breeding of improved lines.

The floral structure of jarrah is similar to other *Eucalyptus* subgen. *Eucalyptus* species, such as *Eucalyptus stellulata* (House 1997, Fig. 1a), and *E. regnans* (Griffin 1980; Griffin & Hand 1979; Griffin *et al.* 1987). Flowers per umbel range between one and eleven, and trees do not usually flower prolifically every year, but have one good flowering season every two or three years. Flower buds are always seen in the autumn but can drop off later in the year.

Anthesis occurs in most eucalypt species 3–28 days prior to the stigma of the same flower being receptive (Griffin & Hand, 1979; Oddie & McComb 1998; Williams 1999). The style elongates following anthesis (operculum lift). While individual flowers are protandrous this does not prevent pollen from one flower pollinating and fertilising another flower on the same tree, and there is

evidence that this occurs in most of the species studied (Elridge *et al.* 1993; Moncur & Boland 1989; Potts and Cauvin 1988; Pryor 1951, 1976).

Detection of stigma receptivity is essential for successful controlled pollination and different indicators of stigma receptivity have been described. The style in *Eucalyptus regnans* lengthens when approaching the receptive period, and the surface of the stigma expands (Griffin & Hand 1979). Receptivity in this species was determined (by the lengthening of the stigma and increased exudate on the stigma) to be between 10 and 14 days after anthesis. Stigma receptivity in three species in Section *Bisectaria* was marked by stigma secretions, coinciding with the greatest number of pollen grains adhering to the stigma surface (Ellis & Sedgley 1992). In *E. woodwardii* (*Eucalyptus* subgen. *Symphomyrtus*), no style elongation was observed during the receptive period, but stigma secretions were maximised when it was most receptive, seven days after anthesis (Sedgley & Smith 1989).

The method most often used for controlled pollination in eucalypts involves emasculation and isolation of flower buds, and frequently, pollen storage (Moncur, 1995). Low fertilisation rates have occurred in several species, and sometimes two controlled pollinations produce more seed. Griffin *et al.* (1987) reported many more fertilised ovules in *E. regnans* after successive pollinations two days apart. Pollen collection is usually from buds at operculum lift stage, and the pollen is sieved and placed in a vial, and stored at or below 0°C. Griffin *et al.* (1982) reported storing pollen from *E. regnans* satisfactorily at room temperature for 36 days, after grinding the anthers to release the pollen in a glass tissue grinder with distilled water. The homogenate was then filtered through a nylon cloth (37μm pore size) then

a millipore filter (3µm) and the pollen on the filter dried over silica gel. Turner *et al.* (1994) kept branches with buds in water for three to five days in the laboratory so that the buds could open and pollen easily collected for processing.

In *E. marginata* pollination is affected by a range of insect and bird vectors (Yates *et al.* 2005). Purple crowned lorikeets have been observed feeding on *E. marginata* flowers (House 1997). A range of insect species have been seen to visit *E. marginata* flowers, such as flies, bees, wasps, beetles and moths (Yates *et al.* 2005), in common with other *Monocalypts* such as *E. regnans* (Griffin & Ohmart 1986). Wind pollination is regarded as being unlikely as a major pollinating vector in *Eucalyptus*. Pollen is thought to be dispersed up to approximately 100 metres (Eldridge *et al.* 1993), and in *E. kochii* sometimes up to 500 metres (Byrne, *pers. comm.*), and, given the evidence from certain natural hybrids, apparently much further in some species (Potts *et al.* 2003).

While it could be expected that similar pollination rates could be seen in *E. marginata* as other eucalypts, as well as capsule production, it is not necessarily the case. This study, while following similar techniques to successful methods used in other species, is surprising in the low levels of pollination success achieved.

Materials and Methods

Trees used

Wild trees (endemic *E. marginata* trees) in the Harry Waring Mammal Reserve (32° 9' 47"S, 115° 49' 22"E), at Wattleup, Western Australia (WA) and clones (developed using tissue culture techniques for resistance to *Phythophthora cinnamomi*, McComb *et al.* 1996) growing at Murdoch University, WA (32° 2' 54"S, 115° 50' 46"E) and Marrinup Orchard, (32° 42' 5"S, 116° 3' 5"E) near Dwellingup, W.A. were used for control pollination experiments. Wild trees were chosen for their similar size to the clonal trees.

Stigmatic Receptivity and Pollination Success

Stigmatic receptivity in *Eucalyptus marginata* was first investigated using clones growing at Murdoch University during November 1998 and February 1999 (hereafter referred to as 1999). This work was further developed during September, October, and November, 2000, and in September/October, 2001 (referred to hereafter as 2000, 2001). Trials were undertaken to detect when stigmas were receptive. Stigma receptivity was determined by assessing the number (and sometimes the length) of pollen tubes in styles observed under microscopic UV light, as outlined in Sedgley & Smith (1989), and Potts and Gore (2000). Numbers of pollen tubes were estimated within a range of five (0 – 5, 5 – 10, etc.) because of the difficulty in making exact counts. Styles were collected 24–72 hours following pollination, fixed in Farmer's Fluid (Acetic Acid: Ethanol 1:3) for approximately one hour, then stored in 70% ethanol. After rinsing in distilled water the styles were slit along their length, then placed in 5% sodium sulphite and autoclaved. When cool, the styles were again rinsed in distilled water, the epidermis was removed, the style

with the stigma placed on a microscopic slide in 1% aniline blue, and gently squashed under a cover slip. This tissue was observed under a fluorescence microscope for pollen tubes (Fig. 1d).

Time of stigmatic receptivity was tested in emasculated and intact flowers by pollinating 0 – 11 days after anthesis in 1999 and 2 – 7 days after anthesis in 2000, 2001 (Table 1). Pollination success variation within the flowering season was observed by comparing pollination success at the early, middle and late periods of the flowering season (20 flowers for two clones for each of the three times using processed pollen). A trial was also conducted to determine whether multiple pollinations of the same flower were advantageous. In jarrah, the flowers were pollinated on day four followed by a repeat pollination on day five after anthesis (20 flowers for two clones using fresh pollen).

Tests of pollination techniques

Preliminary work was conducted in 1999 to test stigmatic receptivity and emasculation and isolation techniques. In 2000 and 2001 a number of trials were conducted to test various aspects of the pollination process using two clones, and two wild trees.

Two pollination techniques were compared. These are: the 'processed' technique after Moncur (1995), and the 'fresh' technique. In each case pollen from several genotypes was used for cross-pollination. The 'processed' technique involved brushing the flowers of several genotypes over a 200mm sieve and collecting pollen in a small bottle with a rubber stopper and storing it at 4°C or at room temperature. Pollen was applied to the stigma using the rubber stopper or a toothpick. Secondly the 'fresh' technique involved wiping a freshly picked flower with the operculum removed across a receptive style. Each style was wiped with several buds from several genotypes. Branches with buds were sometimes picked and kept in water for up to five days in the laboratory, and the flowers used when they were at operculum lift stage. Only pollen with viability over 50% was used, determined by using the method described in Wheeler and McComb (2006). This technique involves germinating fresh pollen *in vitro* using the wettable cellophane technique (Alexander and Ganeshan 1989) with a germination medium of 300 ppm hydrated calcium nitrate, 200 ppm hydrated magnesium sulphate, 100 ppm potassium nitrate and 150 ppm boric acid in 25% maltose (after Brewbaker & Kwack 1963), or a medium of 25% maltose with 150 ppm boric acid (McComb unpub.). Cultures were incubated for 24 – 48 hours, then the pollen tubes were counted under a light microscope.

The clones were tested for differences between self- and cross-pollinated flowers in the numbers of pollen tubes, in the season of 2000, and in 2001 selfed and cross pollinations compared wild trees to clones. To test whether damage to the flowers from the removal of the anthers reduces pollination success, a comparison of pollination success using emasculated and non-emasculated flowers was conducted.

Isolation methods

In 1999 and 2000, the bagging method for isolation was based on Moncur (1995), using double crispy-wrap
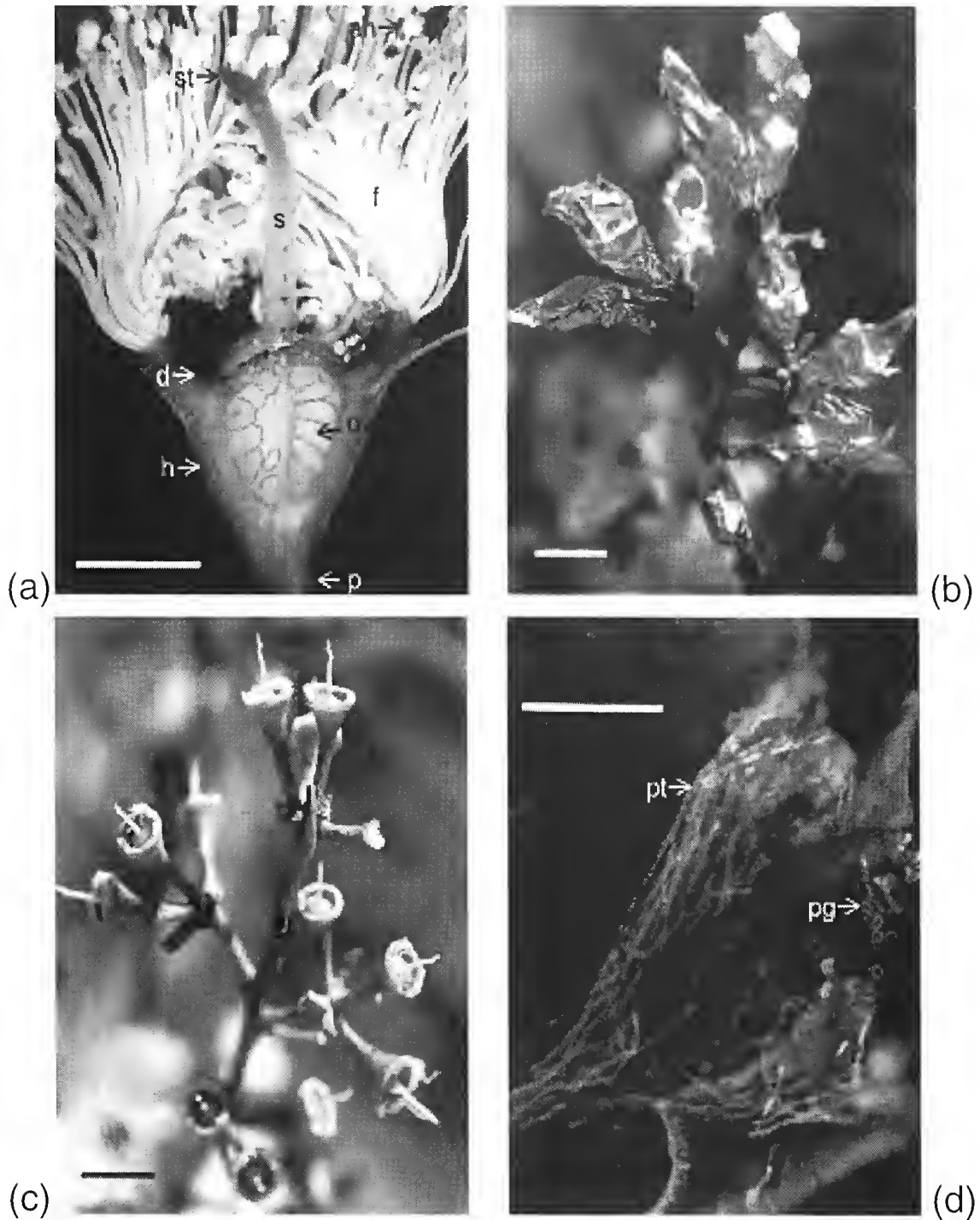
Figure 1. (a). Longitudinal mid-section of a *Eucalyptus marginata* flower at anthesis. Ovule walls have been digitally enhanced. St = stigma, s = style, f = filament, an = anther, d = disc, h = hypanthium, ov = ovule, p = pedicel. Bar = 5 mm. (b). Emasculated flowers of *E. marginata* that have been isolated with foil squares. Bar = 15 mm. (c). Emasculated flowers of *E. marginata*. Extra flowers have been pruned from the branch for the photograph. Bar = 10 mm. (d). Fluorescence image of a squashed *Eucalyptus marginata* style upper section harvested 2 days after controlled pollination and stained with analine blue. Pollen tubes (pt) extend for approximately one third to half the way down the style. Some pollen grains (pg) have not yet germinated. Bar = 100 μm.

bags with a wire coil to prevent damage to the emasculated buds. In 2000, this method was compared to the foil method where aluminium foil squares were cut approximately 4x4 cm and twisted around individual flowers after emasculation. Flowers isolated with foil squares did not require bagging. The aluminium foil squares were removed for pollination, and then replaced (Fig.1b). The foil method of isolation was used in 2001.

Emasculation and pollination

All buds to be pollinated were emasculated at the operculum lift stage, by cutting around the base of the anthers above the hypanthium with a scalpel, then removing all anthers and pollen from the bud, taking care to leave the disc, style and stigma undamaged (Fig. 1c) as described by Griffin *et al.* (1982). In 1999 it was found that flowers exposed to full sun to rarely set fruit

Table 1

Stigmatic receptivity of *Eucalyptus marginata* clones assessed from the numbers of pollen tubes in the style. 3–14 flowers were pollinated with processed pollen for each day followinganthesis ,

Days after anthesis	Range of numbers of pollen tubes (no. of flowers pollinated)		
	Clones (at Murdoch University, 1999)		
	5JN119 (November)	503JP16 (November)	11JN379 (January 2000)
0	0 (10)	0 (10)	0 (10)
1	0 (10)	0 (10)	0 (10)
2	0 (10)	0 (10)	0 (10)
3	1 – 5 (10)	1 – 5 (10)	1 – 5 (10)
4	1 – 5 (10)	1 – 5 (10)	1 – 5 (10)
5	0 (10)	5 – 10 (10)	1 – 5 (10)
6	1 – 5 (10)	Not tested	1 – 5 (10)
7	0 (10)	5 – 10 (10)	0 (10)
9	1 – 5 (10)	1 – 5 (10)	1 – 5 (10)
11	1 – 5 (10)	1 – 5 (10)	0 (10)

Days after anthesis	Clones (at Marrinup, 2000)			
	162A18 (September)	12JN72 (October)	133JN51 (November)	129J55 (November)
4		5 – 10 (4)	20 – 25 (8)	0 – 5 (6)
5	10 – 15 (7)			
6	25 – 30 (5)			
7	15 – 20 (7)			

Days after anthesis	Clones (at Murdoch University, 2000)			
	503JP16 (September)	5JN119 (September)	503JP16 (October)	5JN119 (October)
3	0 (4)	0 – 5 (3)		
4	0 – 5 (3)		10 – 15 (5)	20 – 25 (5)
5	5 – 10 (12)		15 – 20 (13)	15 – 20 (14)
6	0 – 5 (3)			

when hand pollinated (data not shown) so that future work used only partly shaded flowers.

Statistical analysis

Chi-square tests, Wilcoxon matched pairs tests or log linear analyses tests were used at the 0.05 level of significance to test for significant differences (data was not normally distributed, discreet numbers were used in data collection, and sample sizes were small). All factors were fixed.

Results

Stigmatic receptivity

In the 1999 season, pollinating 5 – 7 days after anthesis gave the best results (Table 1) although some pollen tubes were observed in styles between days 3–11 after anthesis. In the 2000 season, pollinating 4–5 days after anthesis gave the most pollen tubes in styles, but best results varied over the flowering period being five days after anthesis in September (58% to 85% of flowers with pollen tubes), 4–5 days in October (58% to 81% of flowers with

pollen tubes) and 4 days after anthesis in November (50% to 63% of flowers with pollen tubes). The interval between anthesis and maximum stigma receptivity apparently decreased as the weather warmed. In December 2001 when the wild trees at Wattleup were flowering, stigmatic receptivity followed four days after anthesis, where 86% to 100% of flowers were successfully pollinated (Table 2).

Pollen processing

The 'fresh' pollinating technique proved to be far more successful than using the traditional processed pollen.

Table 2

Percentage of styles containing pollen tubes in two wild *E. marginata* trees from Wattleup after control-pollination 4 days following anthesis in December 2001.

Tree	Number of flowers	% of styles containing pollen tubes
Wild tree 1	7	86
Wild tree 2	5	100
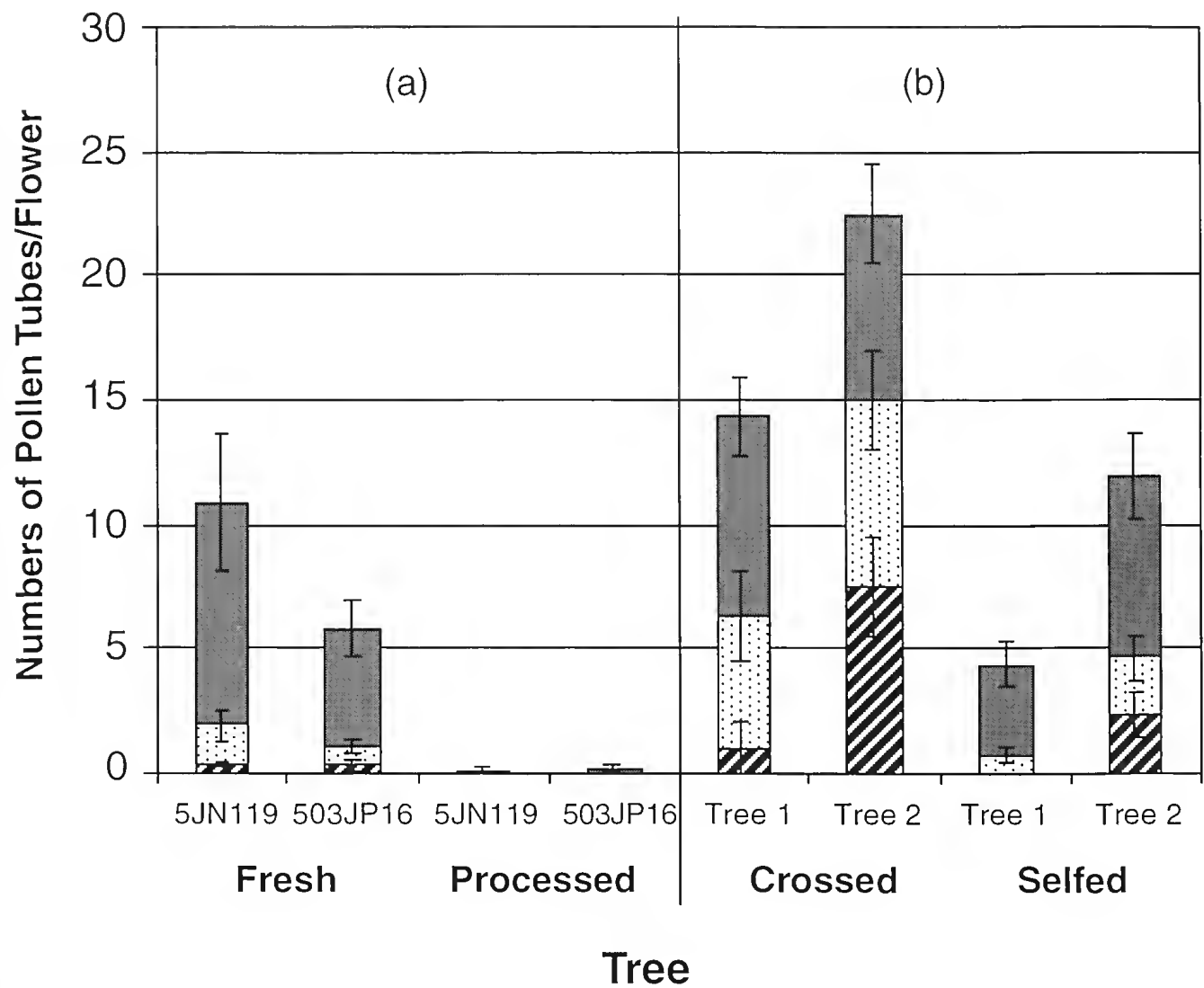
Figure 2. Comparison of mean numbers of pollen tubes in styles as a result of 'processed' and 'fresh' pollination techniques in controlled-pollination of jarrah (clone 5JN119 and 503JP16) flowers (2001 season, 28 flowers for each treatment), and of self- and cross-pollinated wild jarrah trees (2001 season, 3 flowers for each treatment). ■ Represents tubes in the top third of the style; ∴ represents tubes in the middle third of the style; and ▨ represents tubes in the bottom third of the style. Means are shown with standard error. Fresh pollen was used to pollinate buds 4 days after anthesis.

Numbers of pollen tubes in styles were greatly increased by using the 'fresh' technique, and some tubes reached the lower third of the style (Fig. 2). No tubes reached the lower third of the style using the 'processed' technique three days after pollination. A log linear analysis that considered technique, clone and position in the style found significant differences between the two techniques (Chi-square = 560.61, d.f. = 1, p < 0.001), clone (Chi-square = 41.43, d.f. = 1, p < 0.001) and position in the style (Chi-square = 501.32, d.f. = 2, p < 0.001), without any interaction between the three variables. There were also larger numbers of pollen grains adhering to the stigma (a mean of 39.5 pollen grains per style for clone 5JN119, and 17.2 pollen grains per style for clone 503JP16), pollinated using the 'fresh' technique. This is more than double the number seen using the 'processed' technique.

Pollination trials

The method of covering flowers with aluminium foil squares was faster to set up than the traditional method of isolating the branch with bags and wire coils. The foil squares were light, and good insulators from the hot sun. The use of two crispy-wrap bags with a wire coil for isolation tended to result in heat damage to the emasculated buds in the hot weather experienced in south-western Australia during the jarrah flowering season, and the bags were heavy on the small branches sometimes resulting in stem breakage.

From assessment of the number of pollen tubes in the styles there were no significant difference in pollination success between self- and cross-pollinated flowers in the 2000 season (0.05 level of significance, Table 3), but in the 2001 season, there were differences between selfed and crossed pollination results (Chi-square = 7.26, d.f. = 1, p < 0.001) that varied between genotypes (Chi-square = 4.22, d.f. = 1, p < 0.001), using the wild trees at Wattleup (Fig. 2). A log linear analysis with no interaction between the variables found significant differences between pollen tube length (Chi-square = 6.40, d.f. = 2, p < 0.001,), with the out-crossed pollen tubes being longer.

Table 3

Pollination success in self- and cross-pollinated flowers of jarrah clones (2000 season). The 'fresh' pollination technique was used to pollinate buds 4 – 6 days after anthesis.

Clone	% of styles with pollen tubes (no. of flowers pollinated)	
	Selfed	Crossed
503JP16 (Murdoch)	56.3 (12)	68.8 (18)
162A18 (Marrinup)	80.0 (5)	85.7 (6)
5JN119 (Murdoch)	80.0 (9)	66.6 (17)
Mean (& s.e.)	68.1 (7.32)	72.5 (13.51)

Figure 3. Pollination success at three different times over the flowering season of 2001 in two jarrah clones at Murdoch University. ▓ clone 5JN119, and ▒ clone 503JP16. There were 20 flowers in each treatment; means are shown with standard error. 'Processed' pollen was used to pollinate buds.

There were no significant differences in the numbers of pollen tubes between the two clones and two wild trees (Fig. 2). There was no significant difference between double pollinated flowers compared to single pollinations. No mature fruits resulted from the single or double pollinated flowers. No significant differences were found in pollination success between the early, middle and late season pollinations. The middle of the season produced most of the pollen tubes for both clones, with 5JN119 apparently remaining fertile for a longer period over the season.

Within three weeks of pollination wild tree 1 had dropped all the hand-pollinated fruits, but wild tree 2 held ten cross-pollinated fruits for at least eight weeks after pollination. No significant differences were noted between the number of self- and cross-pollinated fruits retained on trees six weeks after pollination (Table 4), but the wild trees held more cross-pollinated fruit than self-pollinated fruit at that point in time.

Very few fruits developed to maturity from all the controlled pollinations. While pollination was achieved in 2000, no hand-pollinated fruits survived longer than three months (Table 4), with the drop-off occurring at a consistent rate over the three months. Low numbers of mature fruits were obtained from the controlled pollinations of clones 5JN119 and 503JP16 in the season of 2001, with an average of 4.7% of pollinated flowers developing into mature fruits (Table 5).

Discussion

This preliminary study suggests that successful control-pollination in *Eucalyptus marginata* may depend on a clearer determination of stigma receptivity and whether it varies from season to season. Observed stigma receptivity extended over 5 – 7 days with the peak of receptivity varying within and between the flowering seasons. Although no significant differences were observed in pollination success at different times of the season the results suggest that there may be greater pollination success in the middle of the season (Fig. 3).

The length of time taken for the pollen tube to reach the base of the style was also not established in this study. A possible reason for so few pollen tubes reaching the base of the style is that the styles were not left long enough on the tree after pollinating. Pound (2002) left the styles from pollinated *E. nitens* flowers on the trees for two weeks before harvesting and squashing. Pollinated styles were left for only two days in this work on *E. marginata*, but ten days probably would have been more appropriate. As Faegri & van der Pijl (1979) note, the

Table 4

Numbers of fruits held by two wild trees and two clones six weeks after self- and cross-pollination (2001 season). 50 flowers were pollinated for each treatment on each tree. Fresh pollen was used to pollinate buds 4 days after anthesis. Wild trees were growing at Wattleup, and clones were growing at Murdoch University.

Tree	Self-pollinated flowers	Cross-pollinated flowers
Wild tree 1	0	0
Wild tree 2	3	13
Clone 5JN119	5	6
Clone 503JP16	6	5

Table 5

Fruits resulting from control-pollinations in jarrah (2001 season). Open pollinated flowers were not emasculated.

Treatment	No. of flowers pollinated	Clone 5JN119 (% of flowers that produced mature capsules)	Clone 503JP16 (% of flowers that produced mature capsules)
Single pollinated	15	0	0
Double pollinated	15	0	2
Open pollinated	20	4	0
Early season	20	0	0
Middle season	25	0	2
End of season	10	0	0
Total	85	4 (4.7)	4 (4.7)

Table 6

Numbers of pollen tubes in *Eucalypt* styles. Data from *E. marginata* is sourced from work completed in 2000 (Table 1).

Eucalypt species	Mean number of pollen tubes observed in style
Eucalyptus marginata	13
E. globulus [1]	270
E. nitens [2]	48
E. woodwardii [3]	490
E. regnans [4]	160

1. Pound *et al.* (2002), 2. Pound *et al.* (2003), 3. Sedgley & Smith (1989), 4. Sedgley *et al.*, (1989).

self-incompatibility systems in plants may allow pollen tubes to grow for several days in the style.

There was no evidence for stylar self-incompatibility in jarrah as there was no significant difference observed in numbers of pollen tubes in styles between self- and cross-pollinated flowers (Table 4). This conforms to findings in other eucalypts (Ellis & Sedgley, 1992; Griffin *et al.*, 1987; and Sedgley *et al.* 1989), except for *E. woodwardii* (Sedgley & Smith, 1989), which showed a reduction in the number of selfed pollen tubes. Numbers of pollen tubes observed in styles were generally low when compared to other eucalypts (Table 6). However, numbers of pollen tubes in styles were increased with the introduction of the 'fresh' pollinating technique, and continued to increase as the work progressed.

The 'fresh' pollen-application technique was shown to be more effective for *Eucalyptus marginata* than the traditional 'processed' pollen method (Fig. 2). Fresh eucalypt pollen has not been widely used with cool temperate species such as *E. regnans* (Griffin *et al.*, 1982), *E. grandis* (Griffin *et al.*, 1982), and *E. nitens* (Moncur, 1995) because it will not germinate prior to desiccation. The hot dry flowering season in the jarrah forest may mean that the pollen is desiccated at anthesis, allowing it to germinate immediately. The 'fresh' technique increased control-pollination success compared to the 'processed' technique. One reason for this may be that sieving the pollen damages it, and another is that the storage overnight of the pollen, either at 4°C or at room temperature, may reduce its fertility (Wheeler 2004).

The low percentage of fruit maturation (4.7%) in the control-pollinations (Table 5) was surprising, and contrasts with other eucalypts where higher fertilisation rates have been achieved through controlled pollinations (Oddie & McComb, 1998; Pound *et al.*, 2002, 2003). The percentage of natural fruit set for clone 503JP16 was less than the percentage of mature fruits produced through controlled pollinations (1.5% for natural fruit set and 4.7% for control pollinated fruit, Wheeler, 2004). Fruit produced from the controlled pollinations was less than seen by Byrne and Stukely (*pers. comm.*) in 1996, who recorded 9.3% for crosses with clone 2J355 and 5.1% with clone 11JN550. They applied pollen with the 'processed' method and isolated flowers with bags and wire coils, methods that are considered here to be inferior to the 'fresh' pollen-application technique and foil isolation technique. They also double pollinated firstly on day three after anthesis and again on day six to day nine

after anthesis, but in this study no advantages of double pollination could be demonstrated. If stigmatic receptivity extends over several days, as is suggested by the work presented here, double pollinating is unlikely to make a significant difference to the seed maturation percentage. Without any other factors being obvious, it is considered most likely that the differences seen within the experiments undertaken here, and between these pollinations and those undertaken by Byrne and Stukely represent female fertility differences between genotypes (Wheeler, 2004). Care must be taken in drawing conclusions when only one or two genotypes are used for research on a species that may contain thousands or even millions of genotypes in its natural distribution. The choice of clones or wild trees that have above average female fertility for use in controlled pollination studies would confirm whether the low fertilisation rates seen here were due to technique or to genotype. Clones also retained a lower proportion of flowers (5.5%) than wild trees (9.3%) from open pollinations to the mature capsules stage (Wheeler 2004), suggesting that there has been a change in the reproductive behaviour during the clonal process.

There are three possible reasons for the low seed maturation percentages seen in *Eucalyptus marginata* clones. The pollination rate (pollen tubes reaching the base of the style) may be low. This requires further investigation leaving the pollinated styles on the tree for longer before harvesting. The fertilisation percentage may be low, or the level of zygote abortion high. Most of the trees used for the controlled pollination work were clonal genotypes that may have different rates of pollination, fertilisation and zygote abortion to the wild trees.

Flowering in adjacent trees tends to be synchronous in *E. marginata*, as has been recorded in *E. regnans* (Griffin, 1980). However, the time of anthesis differed between the clones and the surrounding wild trees in the seasons of 2000 and 2001. The clones at Murdoch University (less than ten kilometres away) flowered approximately three months earlier than the wild trees. The variation in flowering periods between the clones and wild trees was difficult to explain. Clones were derived from wild trees (5JN119 – Harvey, 503JP16 – Nannup, 11JN379 – Yanchep, 162A18 – Collie, 12JN72 – Kirup, 133JN51 – Jarrahdale, 129J55 – Jarrahdale), which with the exception of Yanchep are further south than Perth, yet they flowered much earlier than the neighbouring wild trees in the years 2000 and 2001, so that there was little, if any, overlap in flowering between them. In the years 2000 and 2001, the Murdoch clones had almost completed flowering in the second half of November, but the wild trees nearby and at Wattleup (approximately 10 kilometres away) did not begin flowering until December. Older jarrah trees tended to flower later than younger trees, as seen in *E. regnans* (Ashton 1975), but young wild trees were used at Wattleup, so age should not be a factor in the difference in flowering times between the clones and the wild trees. The soils at Murdoch University are sandy, whereas the wild trees that the clones are derived from all grow on serpentine soils, except for Yanchep. The clones at Murdoch University are not irrigated, so moisture should be approximately equal to the wild trees. There may be

differences in micro-organisms between the clones and wild trees. The differences in climate when the trees were flowering made it difficult to draw conclusions regarding the timing of stigmatic receptivity in the clones and the wild trees.

Future work is required on events at fertilisation and during early zygote development to explain the low levels of seed set following hand-pollination. More detailed stigma examination to determine characteristics and duration of receptivity, as has been undertaken with other species (Ellis & Sedgley 1992; Sedgley & Smith 1989) could also be of value..

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Diatoms and macroinvertebrates as biomonitors of mine-lakes in Collie, Western Australia

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Abstract

Several voids created through open-cut coal mining occur near the town of Collie in the south-west of Western Australia. After mining, the voids fill with fresh water and form mostly acidic wetlands. Five of these mine-lakes were monitored in 1999 using macroinvertebrates and diatoms. On the basis of acidity and water chemistry two groups of wetlands were identified using multivariate analyses; wetlands with low pH (< 4.5), and those with comparatively higher pH (> 4.8). Distinct macroinvertebrate and diatom assemblages were characteristic of each of the wetland groups. Macroinvertebrates including *Orthetrum caledonicum* and *Megaporus solidus* were associated with the Group 1 wetlands (pH < 4.5) while *Sternopriscus browni* and *Micronecta* sp. were two of the most abundant macroinvertebrates in the Group 2 wetlands (pH > 4.8). In the Group 1 wetlands *Nitzschia paleaeformis* and *Pinnularia microstauron* were among the dominant diatom species. *Eunotia curvata* and *Tabellaria flocculosa* were two of the diatom species commonly found in the Group 2 waterbodies. While pH was one of the factors primarily responsible for the distribution of both biomonitors, diatoms appeared to be more sensitive than macroinvertebrates to acidity.

Keywords: Diatoms, macroinvertebrates, pH, mine-void wetlands, biomonitors

Introduction

The continuing loss and degradation of the world's natural wetlands has triggered an increased emphasis on artificial wetlands (Hammer 1992). Pits, or voids, created by mining processes may be rehabilitated to resemble natural habitat or to be used for recreational purposes (John 1993). The Collie Basin, a depression in the Yilgarn Block in South-western Australia has many voids created after open-cut coal mining (Lord 1979) that intercept the aquifer and eventually become wetlands (Brugam & Lusk 1986). The water from artificial wetlands created by mining can be problematic with high acidity and extreme concentrations of heavy metals (John 1997; Kalin *et al.* 2001). The mine-void wetlands of the Collie Basin range in pH from 2–6. Sources of acidity in mine voids can include the unearthing of sulphidic soil (Gambs & Walsh 1981), leaching of mine waste dumps and erosion (Norris 1986). However, the exact cause of acidity in the Collie voids is uncertain although sulphidic soil and organic acids are implicated (John 1997).

Only limited work has been carried out on the biological communities of the Collie void wetlands. Ewington 2, Blue Waters, Stockton Lake, Stockton Tailings Pond and Black Diamond were the five wetlands chosen for this study. Two commonly used biomonitors, macroinvertebrates (Abel 1989; Hellawell 1986; Lenat & Barbour 1994; Rosenberg & Resh 1993) and diatoms (Battarbee *et al.* 1999; Chessman *et al.* 1999; Lepistö 1988) were selected as potential ecological indicators for these

wetlands. Biological monitoring is commonly used as chemical variables lack the responsiveness necessary to assess ecosystem health (John 2003). Chemicals in aquatic systems can undergo wide fluctuations and while chemical monitoring can provide information about the conditions at the time of sampling, it may not detect biologically significant peak concentrations (Abel 1989). Whereas biological monitors such as macroinvertebrates integrate changes in water quality (Sandin, Dahl & Johnson 2004).

The objectives were to identify the macroinvertebrate and diatom assemblages characteristic of the wetlands and to determine species distribution along a pH gradient. A further objective of this study was to determine which group was the most sensitive indicator of acidity.

Analyses of both invertebrate (Courtney & Clements 1998; McNicol *et al.* 1995; Schindler 1990) and diatom communities (Stokes & Yung 1986; Eloranta 1990; Kwandrans 1993; Battarbee *et al.* 1997) have documented shifts in community structure and reduced diversity in response to low pH. Although macroinvertebrates are more frequently used as biomonitors in Australia, studies have shown that diatoms are highly sensitive to water quality changes (John 1993).

Monitoring biodiversity in acid–impacted water bodies has become an integral part of the management strategy for such waters. The use of biomonitors such as macroinvertebrates and diatoms can provide greater understanding of these systems, from the perspective of rehabilitation. Development of ideal tools for biomonitoring the success of converting acidic voids into

functional wetlands may have significant uses throughout Australia.

Methods

Study Site

The town of Collie (32°S, 116°E) is approximately 200km south of Perth, Western Australia. The study sites (Fig 1, Table 1) are located south-east of the town in the Collie Basin, which covers an area of about 274km² (Environmental Protection Authority 1992).

Black Diamond is a large void wetland with boundaries comprising of low gradient shoreline and sections of steep cliff. It possesses a moderate level of riparian vegetation. Blue Waters has similar cliffs to Black Diamond but is a smaller wetland, basically devoid of fringing vegetation. Ewington 2 is relatively small but has a maximum depth of 11 metres. There is a dense stand of sedges growing at the north-east corner of the void. Stockton Lake is one of the larger wetlands sampled with a long cliff face along one side. There are some emergent macrophytes present and it is the only void from which the native fish *Edelia vittata* has been collected. Stockton Tailings Pond is a small wetland with abundant fallen leaves and debris from the peripheral

Table 1

Code and location of void wetlands

Wetland Name	Wetland Code	GPS
Black Diamond	BD	33°20.33s 116°05.58e
Blue Waters	B	33°20.24s 116°13.16e
Ewington 2	E	33°20.48s 116°12.02e
Stockton Lake	S	33°23.13s 116°13.°75e
Stockton Tailings Pond	ST	33°23.13s 116°13.74e

vegetation and a high deposition of iron oxide. It is the only lake out of the five sampled to display extensive macroscopic algal growth. *Mougeotia* sp., a filamentous green alga recognised as a hyperaccumulator of iron and aluminium (John *et al*. 1999), was recorded in abundance in this lake.

Sampling

The sites were monitored monthly between March and July 1999. Electrical conductivity, salinity, pH, temperature and dissolved oxygen were measured using a T.P.S WP-81 Meter and a portable HORIBA Water Quality Checker (U – 10).

Unfiltered water samples were collected from each wetland using acid treated bottles, and were analysed by
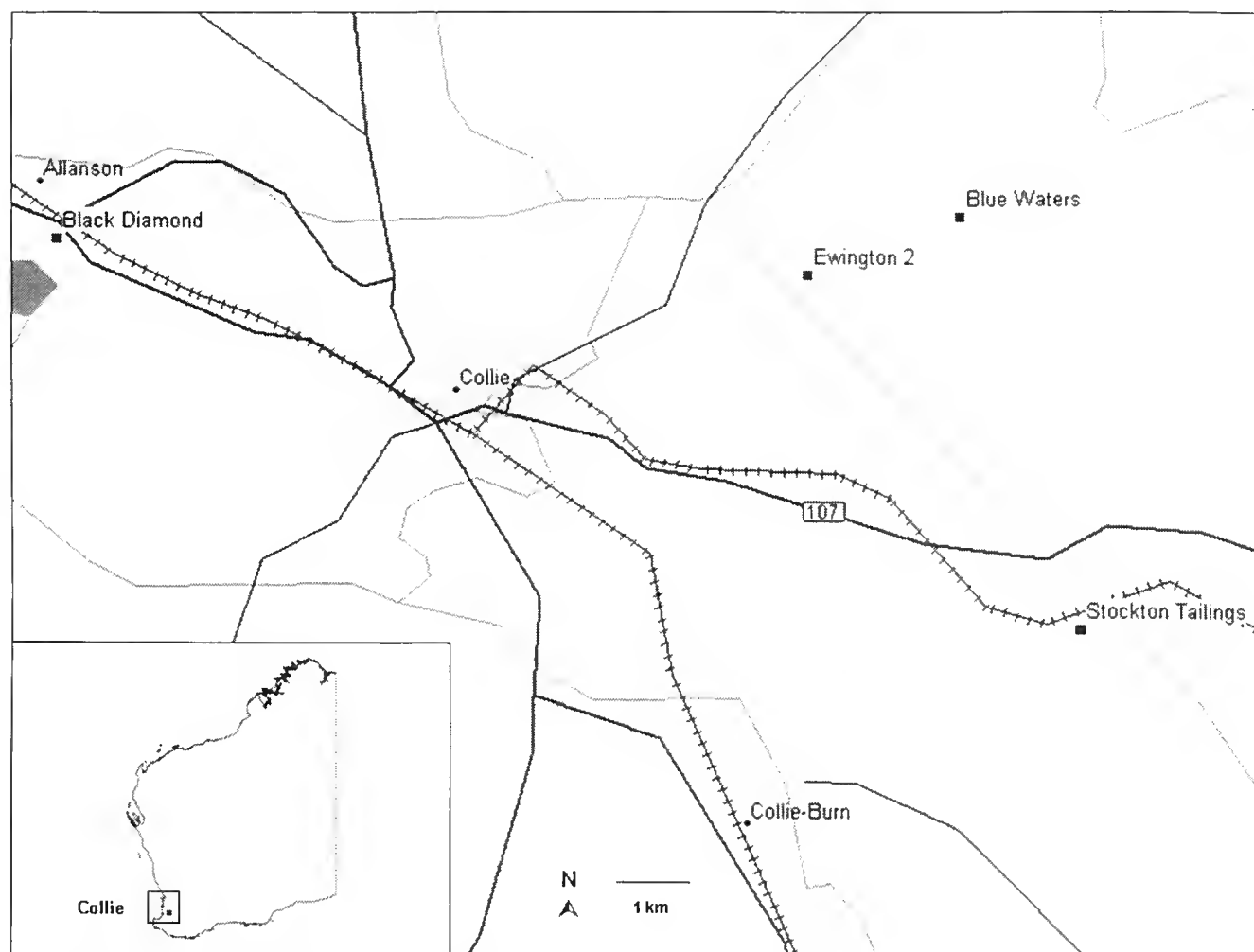

Figure 1. Map showing location of the Collie wetlands.

the Australian Environmental Laboratories (Analabs) Pty Ltd., Welshpool, Western Australia for pH, total alkalinity, calcium, aluminium, iron (soluble), total carbon, total organic carbon, total nitrogen, total phosphorus and chlorophyll α.

Macroinvertebrate and diatom samples were collected fortnightly to monthly. Macroinvertebrates were monitored using a rapid assessment method modified from Chessman 1995. Samples were collected using a 250 µm mesh net with a 400 mm x 280 mm opening. At least three habitats including emergent vegetation and benthos were sampled at each wetland, over a 6 metre transect. The collected material was sieved and specimens live picked for a minimum of 30 minutes, with samples preserved in 10 % formalin. Periphytic diatoms were collected using JJ Periphytometers – to ensure uniform sampling (John 1998). These were fitted with ten glass microscope slides and were fully immersed at the sites. After at least fourteen days, they were retrieved and the slides (with the periphyton) were removed and preserved using Transeau's algal preservative.

Laboratory Methods

Macroinvertebrates were identified to species where possible using specialised literature: Williams (1980), Davis & Christidis (1997), Horwitz (1995), Ingram *et al.* (1997) and Hawking & Smith (1997). All macroinvertebrates present in the samples were counted and the frequency of the different taxa recorded for statistical analyses. The dominant species were photographed using an Olympus Zoom Stereo-microscope and Olympus SC35 Camera. Voucher specimens were deposited in the Department of Environmental Biology, Curtin University of Technology.

The periphytic samples were processed into permanent slides following methods outlined in John (1983). Between 100 and 350 diatom valves were counted for each sample and percentage frequencies calculated for each species. Light micrographs were taken using a Vanox photomicroscope. Identification was carried out using specialised literature (Patrick & Reimer 1966; Foged 1978; John 1983, 1993, 1998). The permanent slides were deposited in the International Diatom Herbarium, School of Environmental Biology, Curtin University of Technology.

Data Analysis

Multivariate analyses were used to classify the wetlands based on environmental parameters and species composition. Ordinations were generated using the statistical package PC-ORD 4. Correlation based principal component analysis (PCA) was conducted to group sites according to environmental variables, while canonical correspondence analysis (CCA) was used to relate species composition to environmental variables. The statistical significance of variables was established using the Monte Carlo permutation test with 999 random permutations. Species abundance data and the water quality parameters of salinity and temperature were $\log_{10}$ transformed prior to statistical analysis.

Univariate analyses were conducted using the statistical package Minitab version 11. Prior to analysis, data was tested using Levene's test for homogeneity of variance and the Kolmogorov-Smirnov test for normality. One-way Analysis of Variance (ANOVA) was employed to test for significant differences between the wetland groups derived from the ordinations, based on species richness and pH.

Results

As shown in Table 2, alkalinity (represented as $CaCO_3$) was low at each of the wetlands with readings of < 5 mgL^{-1}. Stockton Lake and Black Diamond Lake had substantially lower concentrations of aluminium and iron and Stockton Tailings Pond had the highest levels of iron while aluminium was highest at Ewington 2. TN and TP were low in all wetlands. Productivity (as indicated by chlorophyll a concentration) was also low.

All five wetlands were classified as acidic (Table 3). Although the highest salinity and electrical conductivity readings were approximately four times higher than the lowest, all five wetlands were fresh (salinity < 3 ppt). Seasonal differences meant that both temperature and dissolved oxygen displayed a large variation over the sampling period (Table 3).

The environmental data were subjected to principal components analysis to determine the inter-relationship of the wetlands. Ordination resulted in the separation of the sites into two groups, defined by the first two principal components (Fig 2). A large proportion of variance along axis 1 was explained by the variable pH (r = -0.874). Axis 2 was primarily influenced by salinity (r = 0.878).

There was a significant difference between the pH of the two groups according to ANOVA results (P < 0.001, F = 170.89, df = 52). The first group of wetlands possessed a

Table 2

Water chemistry of the five Collie wetlands (Ca – calcium, Al – aluminium, Fe – iron (soluble), TC – total carbon, TOC – total organic carbon, TN – total persulphate nitrogen, TP – total persulphate phosphorous and Chl α – chlorophyll α). Measured in mgL^{-1}

Site	Alkalinity (as $CaCO_3$)	Ca	Al	Fe	TC	TOC	TN	TP	Chl α
Black Diamond	< 5	6.5	0.2	< 0.05	4.1	3.6	0.21	< 0.01	0.0012
Blue Waters	< 5	10	3.4	0.6	2.8	2.4	0.14	< 0.01	0.0049
Ewington 2	< 5	6.4	4.2	1.9	5.2	3.4	0.18	0.04	0.0009
Stockton Lake	< 5	3.6	0.4	0.5	4.5	4.2	1.1	< 0.01	0.0008
Stockton Tailings	< 5	12	2	6.7	2.2	1.9	0.7	< 0.01	0.0025
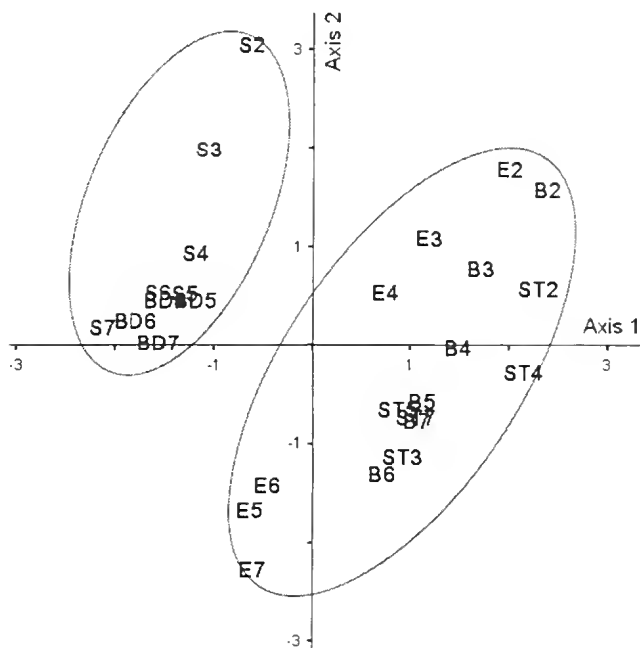
Figure 2. Principal component analysis (PCA) of the Collie wetlands based on environmental variables monitored over the sampling period (March – July). The cluster to the right of the ordination (Group 1) consists of Ewington 2, Stockton Tailings Pond and Blue Waters and represents sites with lower pH values (pH < 4.5). The cluster to top left (Group 2) includes Stockton Lake and Black Diamond Lake and represents sites with pH > 4.8. B – Blue Waters; BD – Black Diamond; E – Ewington 2; S – Stockton Lake; ST – Stockton Tailings Pond. The numbers 2–7 indicate the sampling occasion.

mean pH of 3.96 ± 0.39 while the second group possessed a mean of 5.29 ± 0.26.

The differences in the distribution of invertebrate taxa in the wetlands were determined by canonical correspondence analysis (CCA). Axes 1 and 2 of the CCA explained 18.5% of the total variance in macroinvertebrate distribution (Fig 3). The eigenvalues of axes 1 and 2 were both significant ($P < 0.01$) with values of 0.385 and 0.220 respectively. There was a strong relationship between macroinvertebrate community structure and water quality parameters that was supported by the high species-environment correlations of axis 1 ($r = 0.935$) and axis 2 ($r = 0.837$). Axis 1 was primarily related to pH and salinity, separating the wetlands into two main groups. Group 1 comprised of wetlands with acidic pH (< 4.5) while the Group 2 wetlands possessed comparatively higher pH levels (> 4.8) and lower salinity concentrations.

Although differences were detected in the macroinvertebrate assemblages present, the ANOVA determined that there was no significant difference between the species richness of the two groups ($P > 0.05$, F = 1.21, df = 25), with mean values of 7.67 ± 3.12 and 8.59 ± 3.28 respectively.

Invertebrate taxa that dominated the wetland groups are listed in Table 4. Eight invertebrate taxa were identified as dominant in Group 1 wetlands, with adult coleopterans accounting for the largest proportion. Coleopterans also dominated the Group 2 wetlands with three of the five most commonly occurring invertebrates belonging to this order. Some overlap of dominant taxa was evident between the two groups with the hemipteran *Micronecta* sp., the coleopteran *Necterosoma darwini* and the crustacean *Perthia* sp. inhabiting both wetland types.

Canonical correspondence analysis of the diatom data showed that 35.3% of the total variance in community
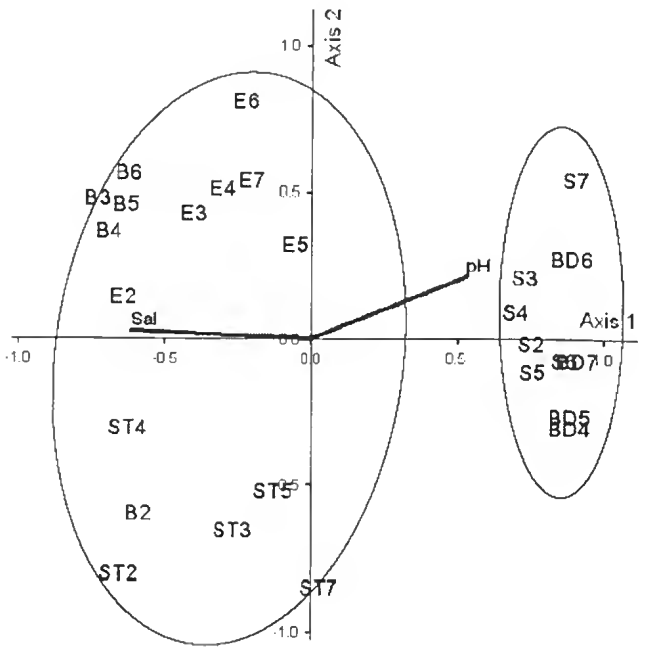
Figure 3. CCA biplot showing wetlands and water quality parameters. The ordination is based on sites, the parameters of pH, dissolved oxygen, $\log_{10}$ salinity, $\log_{10}$ temperature and $\log_{10}$ macroinvertebrate abundance data. Bold lines represent primary water quality parameters separating the two groups. B – Blue Waters; BD – Black Diamond; E – Ewington 2; S – Stockton Lake; ST – Stockton Tailings Pond. The numbers 2–7 indicate the sampling occasion.

Table 3

The range of water quality parameters from Collie wetlands sampled. EC – Electrical Conductivity; DO – Dissolved Oxygen. Numbers of sampling occasions: Black Diamond – 4, Blue Waters – 6, Ewington 2 – 6, Stockton Lake – 6, Stockton Tailings Pond – 5

Site	pH	EC (mS/cm)	Salinity (ppt)	Temp (°C)	DO (ppm)
Black Diamond	4.89 – 5.38	385 – 422	0.21 – 0.23	12.6 – 16.2	7.15 – 8.10
Blue Waters	3.43 – 4.14	1180 – 1931	0.66 – 0.94	12.9 – 22.6	7.28 – 9.01
Ewington 2	3.79 – 4.38	937 – 1465	0.51 – 0.65	12 – 22.1	6.22 – 9.25
Stockton Lake	5.01 – 5.93	393 – 487	0.20 – 0.25	12.5 – 21.4	7.23 – 8.99
Stockton Tailings	3.11 – 3.5	858 – 1285	0.51 – 0.70	12 – 22.9	7.05 – 8.87

Table 4

List of invertebrate taxa recorded from the two groups of wetlands (taxa included were present at > 20% frequency). a indicates adult Coleoptera.

| Group 1 Taxa (pH < 4.5)	Group 2 Taxa (pH > 4.8)
Anisops sp.	*Micronecta* sp.
Diplacodes bipunctata (Burmeister)	*Necterosoma darwini* (Babington) a
Megaporus howitti (Clark) a	*Perthia* sp.
Megaporus solidus (Sharp) a	*Sternopriscus browni* (Sharp) a
Micronecta sp.	*Sternopriscus maedfooti* (Clark) a
Necterosoma darwini (Babington) a	
Orthetrum caledonicum	
Perthia sp.	
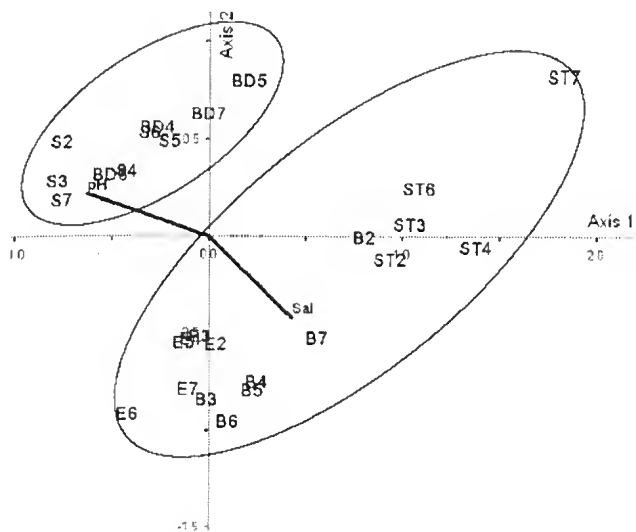
Figure 4. CCA biplot showing wetlands and water quality parameters. The ordination is based on sites, the parameters of pH, dissolved oxygen, $\log_{10}$ salinity, $\log_{10}$ temperature and $\log_{10}$ diatom abundance data. Diatom species included were those with a maximum abundance of > 1%. Bold lines represent primary water quality parameters separating the two groups. B – Blue Waters; BD – Black Diamond; E – Ewington 2; S – Stockton Lake; ST – Stockton Tailings Pond. The numbers 2–7 indicate the sampling occasion.

structure was explained by the first 2 axes (Fig 4). With eigenvalues of 0.475 and 0.297 respectively, both axis 1 and axis 2 were significant ($P < 0.01$). High species-environment correlations for axis 1 ($r = 0.893$) and axis 2 ($r = 0.887$) displayed the strong relationship between diatoms and water quality parameters, similar to that demonstrated by macroinvertebrates (Fig 3). pH and

salinity were the two factors most closely related to axis 1 and were the primary factors determining the separation of the wetlands into two groups (Fig 4).

Diatom species richness varied significantly between the two groups. ANOVA determined that the mean taxa numbers of the Group 1 wetlands (8.46 ± 2.60) were significantly lower ($P < 0.001$, F = 109.29, df = 52) than the Group 2 wetlands (16.39 ± 2.64). Six species were identified as the most commonly occurring taxa in the first group while eight species dominated the diatom flora of Group 2 (Table 5). There was a limited amount of overlap between the two groups as *Brachysira brebissonii* and *Achnanthidium oblongella* were abundant in both the Group 1 and Group 2 wetlands.

Discussion

Water Quality

Waters affected by mining processes are often highly acidic (Brugam & Lusk 1986; John 1997) consistent with the pH (< 4.5) of Ewington 2, Blue Waters and Stockton Tailings Pond (Group 1). Although the pH of Stockton Lake and Black Diamond (Group 2) were relatively low they were comparatively higher than the Group 1 wetlands (pH > 4.8). Stockton Lake and Black Diamond were further differentiated from the other wetlands by lower salinity, which in conjunction with pH contributed to the separation of the wetlands into two groups in the multivariate analyses. Lower concentrations of inorganic ions were another distinguishing feature of the Group 2 wetlands. Acidification is related to elevated levels of certain metals (Lydén & Grahn 1985) with high concentrations of inorganic ions including calcium, magnesium, sulphate and aluminium common to waters

Table 5

Dominant diatom taxa recorded from the wetland groups (taxa included were present at > 20% frequency).

Group 1 Taxa (pH < 4.5)	Group 2 Taxa (pH > 4.8)
Achnanthidium oblongella (Oestrup)	*Achnanthidium oblongella* (Oestrup)
Brachysira brebissonii (Ross)	*Brachysira brebissonii* (Ross)
Epithemia sorex (Kütz.)	*Eunotia curvata* (Kütz.) Lagerst
Navicula aff. *cari* (Ehr.)	*Eunotia exigua* (de Breb.) Grun.
Nitzschia paleaeformis (Hust.)	*Frustulia* sp.
Pinnularia microstauron (Ehr.)Cl.	*Rhopalodia gibberula* (Ehr.) O. Müller
	Surirella tenera Greg.
	Tabellaria flocculosa (Rabh.) Kütz.

affected by mining (John 1997). The lower concentrations of inorganic ions at the Group 2 lakes as opposed to Group 1 support these findings. The reasons for the differences in water chemistry may be related to age of the wetlands. Black Diamond and Stockton Lake were terminated as mines in 1953 and 1957 respectively and subsequently filled with fresh water (Stronach 1988) and have naturally undergone neutralisation to some degree. Blue Waters and Ewington 2 remained operational for several years after the closure of Black Diamond and Stockton Lake (Ashton 1988).

Macroinvertebrates

The majority of the eight invertebrate taxa identified as dominant in Group 1 (pH < 4.5) belonged to the order Coleoptera. Hemipterans, anisopterans and amphipods were also common. Although the abundance of these taxa in the Group 1 voids might imply that they would be useful indicator species, labelling them as characteristic of low pH waters would be premature. Firstly, there was an overlap between the dominant taxa of the Group 1 and Group 2 (pH > 4.8) waterbodies. The adult coleopteran *Necterosoma darwini* (a) was abundant in both wetland types while the amphipod *Perthia* sp. and the hemipteran *Micronecta* sp. followed a similar pattern of distribution.

Secondly, none of the dominant taxa are restricted to acidic waters. *Megaporus solidus, Megaporus howitti* and *Necterosoma darwini*, the three adult coleopterans that commonly occurred in the Group 1 voids, have been found in wetlands of the Swan Coastal Plain over a range of pH (Balla & Davis 1993; Davis & Christidis 1997). For example, Davis & Christidis (1997) recorded *Megaporus howitti* from Lake Jandabup and North Lake. pH levels of between 4 and 5 have been documented at Lake Jandabup (Sommer & Horwitz 2001) while North Lake is generally considered alkaline (Davis & Rolls 1987).

The crustacean *Perthia* sp. was another of the dominant taxa in the Collie wetlands. Cheal *et al.* (1993) noted that the two recognised species of *Perthia* were only in coloured wetlands. The high levels of humic and fulvic acids in highly coloured wetlands are known to contribute to lower pH (Schmidt & Rosich 1993). The findings of that study in conjunction with those of the current project indicate that *Perthia* may be tolerant to low pH. However the occurrence of *Perthia acutitelson* in Lake Yangebup (Williams & Barnard 1988), a lake identified as having high alkalinity by Growns *et al.* 1993, shows that the taxon may not be reflect acidic conditions.

Micronecta sp. was also abundant in the Collie voids. However, the use of this taxon as an indicator of acidity would be misleading as previous studies have recorded species of this genus from many wetlands in south-western Australia. While *Micronecta robusta* was reported from lakes of the Perth region: Thomsons Lake, Lake Joondalup, Lake Monger, North Lake and the acidic Lake Jandabup, they were most common in the alkaline waterbodies of Lake Monger and North Lake (Davis & Rolls 1987).

Five taxa dominated the invertebrate assemblages of the Group 2 lakes with adult coleopterans and hemipterans comprising the abundant taxa. There was a similar situation with the dominant invertebrates of the Group 2 waterbodies. None of the taxa abundant in the Group 2 lakes are restricted to those pH levels and their use as indicator species would be questionable. For example, *Necterosoma darwini* has been collected from acidic wetlands such as Lake Gnangara (Growns *et al.* 1993) through to relatively neutral lakes including Nowergup Lake and Bartram Swamp (Balla & Davis 1993). Furthermore this coleopteran was also commonly found in the highly acidic Group 1 wetlands of the present study.

The invertebrate taxa abundant in the Collie wetlands are probably opportunistic in nature. The voids are generally lacking in predators and some have stands of peripheral vegetation, two factors which may provide incentive for invertebrate inhabitants. Therefore, while the invertebrates present may be tolerant rather than indicative of the water quality conditions, they do provide insight into the functionality of the wetlands.

Diatoms

Brachysira brebissonii, Nitzschia paleaeformis and *Pinnularia microstauron* were among the most abundant diatom species in the Group 1 wetlands. *Brachysira brebissonii* was noted by Foged (1978) as acidophilous; acidophilous being species which generally occur at pH < 7 but may be found in waters of around pH 7 (Hustedt 1937–1939). John (1993) documented *Nitzschia paleaeformis* in acidic sand mining voids at Capel, Western Australia while Watanabe & Asai (2004) recorded the species from acidic waters in Japan. *Pinnularia microstauron* was identified from waters of pH 5–6 during work on east African diatoms by Gasse (1986). This species seems to prefer slightly acidic water although it can tolerate a range of pH (Patrick & Reimer 1966). The preference of these diatom species for low pH conditions is supported by their dominance in the Group 1 voids of Collie.

Although most dominant species in the Group 1 wetlands were acidophilous, the remaining two species *Achnanthidium oblongella* and *Epithemia sorex* favour alkaline conditions (Foged 1979). *Epithemia sorex* is also known to prefer waters of high conductivity (Patrick and Reimer 1975). Given the low pH of the wetlands, this suggests that the presence of the species in the Group 1 wetlands is probably due to the higher salinity/conductivity of the group in comparison with Group 2. *Achnanthidium oblongella* was described as alkaliphilous by Foged (1978 & 1979); alkaliphilous being species which may occur at pH 7 but generally occur at pH > 7 (Hustedt 1937–1939). However a study of diatoms in New Zealand showed that 11 of 45 locations from which *Achnanthidium oblongella* was collected had pH levels of between 4.5 and 6.4 (Foged 1979). These findings along with those of the current project suggest that while the species may prefer alkaline waterbodies it has a reasonable tolerance to lower pH.

Although most of the dominant diatom taxa of Stockton Lake and Black Diamond (Group 2) are acidophilous, there is a higher proportion of the abundant alkaliphilous species in comparison to the Group 1 wetlands. *Achnanthidium oblongella, Rhopalodia gibberula* and *Surirella tenera* have all been described as alkaliphilous (Foged 1978). The tolerance of

Achnanthidium oblongella to different pH levels was established earlier and presents a possible explanation for its dominance in both wetland types. *Rhopalodia gibberula* was described by Patrick and Reimer (1975) as one that appeared to prefer water with some chloride. Given that the Group 2 wetlands possessed relatively low salinity and conductivity the abundance of *Rhopalodia gibberula* seems incongruous, but Patrick and Reimer (1975) also noted that the species may be found in waters of low conductivity and is widely tolerant. The dominant acididophilous species included *Tabellaria flocculosa* (DeNicola 1986 and Ford 1986) and *Eunotia exigua* (Renberg *et al.* 1985; Ford 1986) and *Eunotia curvata* (Patrick & Reimer 1966).

There was a limited overlap of dominant diatom species between the two groups of wetlands. The acidophilous *Brachysira brebissonii* was abundant in both wetland types while the tolerant *Achnanthidium oblongella* was also dominant in both groups.

Species Richness

Macroinvertebrate taxonomic richness is progressively reduced with declining pH and as acid sensitive species are lost they are replaced by a few acid tolerant taxa (McNicol *et al.* 1995; New 1995). For example Courtney and Clements (1998) identified significantly fewer taxa at pH 4.0 than in waters with pH 5.5 and 6.5. In the present study, there was no pattern of species reduction with declining pH. In contrast, the numbers of diatom taxa in the two groups of wetlands supported findings reported in the literature (Haworth *et al.* 1990; DeNicola 2000; Poulíčková *et al.* 2001; Tipping *et al.* 2002).

Macroinvertebrates and Diatoms as Biomonitors

It has been stated that macroinvertebrates are useful biomonitors of water quality due to their sensitivity (Dills & Rogers Jr 1974). The results of the current study partly support this statement with invertebrate species composition differing between the wetland groups. The lack of relationship between macroinvertebrate species richness and pH and the overlap of dominant species between the Group 1 and Group 2 wetlands both dispute the sensitive response of invertebrates to pH.

The major disadvantage of using macroinvertebrates as biomonitors may be that certain species do not respond to all environmental impacts. Invertebrate abundance and distribution can be influenced by factors other than water quality (Rosenberg & Resh 1993). For example physical factors such as channel width (Soininen & Könönen 2004), substratum (Sládecek *et al.* 1982), season (Lenat & Barbour 1994) and vegetation (Crowder & Cooper 1982) can all affect the species composition of invertebrates.

Aquatic diatom assemblages are known to reflect the water quality (Denys & van Straaten 1992). Diatoms are more sensitive to environmental variables than most other aquatic organisms (John 1998) and the strong relationship between diatom distribution and pH has been recognised for decades (Battarbee *et al.* 2001). The documented sensitivity of diatoms to changing pH is generally supported by the results of the study, with clear groupings of diatom assemblages in wetlands with differing pH. The differences in the diatom assemblages

reiterate the well-defined ecological tolerances of diatoms and their sensitivity to changes in water chemistry such as decreasing pH (Charles 1985; Siver *et al.* 2004). The exhaustive autecological information available on diatom taxa should be an advantage for their use as ideal biomonitors.

Although dominant invertebrate and diatom taxa were identified for the Group 1 and the Group 2 wetlands, the results suggest that diatoms were more sensitive to acidity than were invertebrates. The overall community structure of invertebrates was influenced by pH but none of the dominant species were unique to wetlands displaying water quality similar to that of the Collie waterbodies. The composition of diatom assemblages was also affected by pH but, unlike the invertebrates, most dominant species of diatoms in the Group 1 waterbodies exhibited narrow tolerances to pH and could be used as biomonitors for acidity. The diatom assemblages in the Group 2 wetlands represent a shift in dominance. While most of the dominant species preferred waters below pH 7, Group 2 wetlands maintained a higher proportion of alkaliphilous species in comparison to the Group 1 wetlands. This was probably in response to the higher pH of Group 2 given that as pH moves closer to neutral, species with less defined tolerances can inhabit the waterbodies.

Further research will be helpful to fully examine the merits of macroinvertebrates and diatoms as biomonitors for acidic void wetlands. Future sampling regimes should be expanded to include the measurement of parameters that may influence macroinvertebrates such as peripheral vegetation and sediment characteristics. In terms of diatoms, an aspect that warrants further consideration is the lack of top down effect due to limited algal grazers, and how this might influence biomass and community composition. The incorporation of these variables would provide greater insight into the factors that may influence distribution of the two biomonitors.

Given that a healthy ecosystem comprises of abiotic characteristics and biotic communities (Loeb 1994) an integrated approach using macroinvertebrates and diatoms may be the most effective means of assessing acid waters such as the Collie wetlands. Currently the authors are developing a predictive model that will be applicable for the evaluation and management of similar mine-voids throughout Australia.

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Asplenium aethiopicum recolonises karri forest following timber harvesting and burning

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Abstract

Occurrence of the fern Asplenium aethiopicum (Burm.f.) Bech. was surveyed systematically in 7 ha of karri (Eucalyptus diversicolor) forest that formed part of a larger stand regenerated by clearfelling and burning in 1972. Much of the study area had also been thinned in 1984 to a range of densities (200–600 stems ha^{-1}) to investigate tree and stand growth responses. A. aethiopicum was recorded as an epiphyte growing on large ground logs and stumps in 12 of 28 plots examined during the survey, including a number that had been thinned. Large, partly decayed logs covered in dense moss provided favourable conditions for establishment and growth of A. aethiopicum. The most likely mechanism for re-establishment of A. aethiopicum in the regenerated forest is dispersal from adjoining undisturbed forest, rather than from plants persisting within the harvested area.

Introduction

Unlike tall open eucalypt forests in high rainfall areas of south-eastern Australia, ferns are poorly represented in the flora of the karri (Eucalyptus diversicolor) forest. In south-western Australia ferns are typically confined to moist sites around granite outcrops and permanent watercourses, with the notable exceptions of Lindsaea linearis Sw. which is common on moist sandy soils south of the Blackwood River and the bracken fern (Pteridium esculentum G. Forst. Cockayne) which occurs widely throughout higher rainfall areas on a range of soil types (Wheeler et al. 2002). The impoverished fern flora and absence of species typically associated with temperate rainforest (for example Nothofagus) have been attributed to a history of periodic aridity and fire in south-western Australia during the mid to late Tertiary (Bowman 2003, Hopper 2003).

Asplenium aethiopicum (Burm.f.) Bech. is a cosmopolitan fern with a widespread but scattered distribution that includes southern Australia, tropical and southern Africa, India and Sri Lanka (Brownsley 1998). In south-western Australia the distribution of A. aethiopicum corresponds broadly with that of the karri forest, with outlier populations at Collie and along the southern coast (www.naturebase.net/ florabase/ index.html). A. aethiopicum is most commonly associated with moist crevices around granite outcrops but has also been recorded as an epiphyte on the bark of Allocasuarina decussata (Wheeler et al. 2002). The bark of A. decussata is corky and becomes deeply furrowed if unburnt for several decades. The conservation status of A. aethiopicum in Western Australia is currently Priority Four (Rare Taxa) indicating that it has been adequately surveyed, and while still rare, is not considered to be currently threatened by identifiable factors (Atkins 2005). Such taxa require regular monitoring.

Disturbances that expose the soil and understorey layers of the forest to greater drying by sun and wind may potentially disadvantage species such as A. aethiopicum that depend on sheltered moist sites or on substrates provided by other plants (i.e. bark). Hickey (1994) reported that epiphytic ferns in Tasmanian mixed forest containing eucalypt and temperate rainforest elements were more abundant in stands regenerated by high intensity wildfire than in stands regenerated using silvicultural treatment involving clearfelling, burning and sowing with eucalypt seed. Studies by Wapstra et al. (2003) and Courtney et al. (2005) have also recorded declines in the abundance of epiphytic ferns following clearfelling of wet eucalypt forest in Tasmania.

This note reports the findings of a systematic search for A. aethiopicum undertaken in a regrowth stand of karri that was regenerated in 1972 and then thinned at an age of 12 years for silvicultural research purposes.

Methods

The study was undertaken in Warren forest block 12 km south-west of Pemberton. Average annual rainfall is 1400 mm, with potential summer evaporation of 450 mm (December to February). The study site is located on a broad ridge at an elevation of 120 m a.s.l. and forms part of a 320 ha compartment of forest regenerated in autumn 1972 following clearfelling for sawlogs. Karri was the dominant overstorey tree in the original mature forest, with occasional marri (Corymbia calophylla). High intensity post-harvest burning was used to prepare receptive seedbed and stimulate release of seed from retained mature karri trees (Fig. 1). Seed trees were removed later in 1972 and very few living or dead trees

Figure 1. Photograph taken following the high intensity regeneration burn at Warren block in 1972.

from the original forest remained standing at the time of measurement in 2005. Residual logs unsuitable for sawmilling were retained on site, including a number of large diameter fallen karri trees with severe scarring on the stem and internal wood defect.

Seven ha of the regrowth forest were thinned in 1984 for a silvicultural experiment designed to investigate the effects of early thinning on stand growth. The experiment included 28 contiguous 50 m x 50 m plots of which four were retained as unthinned controls and the remainder non-commercially thinned to densities of 200, 400 or 600 stems ha⁻¹. Thinning treatments were assigned randomly to individual plots in the experimental design. Coppice regrowth from karri stumps was controlled two years after thinning with a one-off application of herbicide to half of the thinned plots. Fire has been excluded from the regrowth forest at the study site since 1972.

During routine re-assessment of the thinning trial in April and September 2005 three observers systematically searched each plot for *A. aethiopicum*. Observers walked throughout each plot to locate and measure trees and took additional time to search for *A. aethiopicum* on ground logs, stumps and other potential substrates. On average the team of observers spent 3 hours measuring and searching each plot.

Results

The regrowth stand was 33 years old in 2005 and codominant trees were 40–45 m tall. In unthinned plots

Figure 2. *A. aethiopicum* growing in deep moss on a large diameter karri log.

the density of live karri trees ranged from 900 to 1000 stems ha^{-1} and the understorey had largely senesced and collapsed to form a layer of woody material suspended above the leaf litter layer on the forest floor. Bracken, *Trymalium floribundum* and *Chorilaena quercifolia* were present in all plots, sometimes forming a dense understorey in the heavily thinned plots where overstorey canopy closure was incomplete.

Individual plants and small groups of *A. aethiopicum* were recorded in 12 of the 28 plots. Deep moss beds on large karri ground logs (>1 m diameter) were the favoured substrate and supported both the greatest number of *A. aethiopicum* plants, and the largest individuals some of which had multiple fronds up to 0.3 m in length (Fig. 2). A small number of plants were also observed growing in moss beds that had developed on cut stumps from the original mature forest. No *A. aethiopicum* plants were observed growing on small diameter karri logs resulting from the thinning operations in 1985 (<0.3 m diameter), on the bark of *A. decussata* saplings, or in the litter layer on the forest floor. *A. aethiopicum* occurred in 3 of the 4 unthinned plots, and in a number of thinned plots including some that had been subject to coppice control treatment (Table 1). There was no clear relationship between occurrence of *A. aethiopicum* and thinning or coppice control treatment.

Discussion

The findings of this survey demonstrate that *A. aethiopicum* is capable of recolonising karri forest within 3 decades of major disturbance from timber harvesting and fire. Although this is the first systematic survey for *A. aethiopicum* to be undertaken at the site, herbarium voucher specimens collected previously from the same location indicate that recolonisation had commenced by the time the stand was 25 years old. Individual plants of *A. aethiopicum* are unlikely to have persisted in-situ from the original mature forest because of the high level of disturbance associated with clearfelling and burning operations in 1972. Spore dispersal from plants in adjacent areas of undisturbed mature forest is the most likely source of propagules for recolonisation of the regenerated forest. The closest mature forest is about 400 m from the study site. Hickey (1994) suggested that

Table 1

Occurrence of *A. aethiopicum* in plots subject to a range of thinning and coppice control treatments.

Stand density	Coppice control	No. of plots	No. of plots where *A. aethiopicum* was recorded
Unthinned	N/a	4	3
600 stems ha^{-1}	No	4	4
	Yes	4	1
400 stems ha^{-1}	No	4	0
	Yes	4	1
200 stems ha^{-1}	No	4	0
	Yes	4	3

epiphytic ferns may recolonise stands regenerated by clearfelling provided that there is adequate spore dispersal and suitable micro-sites develop prior to the next disturbance. In Tasmania, vascular epiphytes associated with late-successional stage forests may take up to 5 decades to recolonise logged substrates (Peacock & Duncan 1994).

Critical factors in the regeneration of karri include preparation of a receptive seedbed of ash or mineral soil, stimulation of seedfall and temporary removal of competition from understorey shrubs and overstorey trees (Loneragan & Loneragan 1964, Christensen 1971). Since the late 1960s, timber harvesting operations in mature karri stands have utilised a silvicultural system based on clearfelling of the overstorey followed by an intense slash burn in late spring to early autumn, with regeneration established by seedfall from retained mature trees or by planting seedlings raised in a nursery (White & Underwood 1974, Breidahl & Hewett 1995). No specific actions have been implemented to facilitate the regeneration of other eucalypts that co-occur with karri (e.g. *E. marginata*, *E. patens*, *C. calophylla*) or the regeneration of understorey plants, except on heavily disturbed sites such as log landings. Wardell-Johnson *et al.* (2004) examined floristic patterns in an age sequence of karri stands disturbed by fire and timber harvesting, and concluded that the vascular flora of the karri forest is comparatively resilient to the effects of these disturbance factors. Quadrat-based species richness (α diversity) was highest in recently burnt sites due to the influx of short-lived annuals and ephemerals, and lowest for sites having intermediate disturbance intervals (11–20 years) which were dominated by a small number of woody shrubs including *T. floribundum*, *C. quercifolia*, *Bossiaea aquifolium* subsp. *laidlawiana* and several species of Acacia (Wardell-Johnson *et al.* 2004). These shrubs all regenerate from soil stored seed and persist for several decades before declining to relatively low densities (<0.5 m^{-2}) in the absence of further disturbance (McCaw *et al.* 2002).

Differences in occurrence of *A. aethiopicum* between plots are likely to reflect the availability of large ground logs with a well developed moss layer and the current distribution of *A. aethiopicum* within the study area may be influenced by the spatial pattern of ground logs resulting from clearfelling of the mature forest. Large ground logs are now recognised as an important legacy of mature forests (Lindenmayer *et al.* 2002). Over the past two decades there has been a progressive reduction in the size of clearfell patches in karri forest and an increased emphasis on retention of mature habitat components both within harvested areas and throughout the landscape (Anon. 2004). These management actions should accelerate re-colonisation of disturbed sites by *A. aethiopicum* and other species that rely on dispersal by spores. Subsequent disturbance of the regrowth forest in 1984 by thinning and coppice control has not prevented *A. aethiopicum* from recolonising suitable substrates in thinned plots.

In the longer term, the population dynamics of *A. aethiopicum* in regrowth karri forest will also be influenced by the frequency, intensity and seasonality of fire.

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Synaphea xela (Proteaceae: Conosperminae), a new species from the Jurien-Eneabba area of south-west Western Australia

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Abstract

Synaphea xela R. Butcher is described here as new and differentiated from similar species and regional congeners. *Synaphea xela* is restricted to the Jurien-Eneabba area of Western Australia and is currently known from only three populations over an area of approximately 55 km². A Conservation Code of Priority Two is considered appropriate for this species based on the paucity of collections and the high level of species endemism in this region.

Keywords: *Synaphea*, Proteaceae, Southwest Australian Floristic Region, kwongan, taxonomy.

Introduction

The Southwest Australian Floristic Region (SWAFR) is recognised for its extraordinarily high levels of species diversity and endemism (Myers *et al.* 2000, Hopper & Gioia 2004), especially among the large Gondwanan families Proteaceae, Restionaceae and Myrtaceae (Paczkowska & Chapman 2000, Hopper & Gioia 2004). Within Proteaceae, 16 genera comprising 869 formally recognised species and subspecies (99% endemic) are recorded as occurring within the 302 627 km² comprising the SWAFR (Cowling & Lamont 1998), with many large (*e.g. Grevillea, Hakea, Banksia/Dryandra sensu* Mast 1998, Mast *et al.* 2005) and moderately large (*e.g. Conospermum, Petrophile, Synaphea, Isopogon*) genera having undergone massive *in situ* diversification leading to the production of species flocks (Cowling & Lamont 1998).

Two major centres of species richness have been identified for Proteaceae within the SWAFR; the first occurring on the northern sandplain and centred on the Mt Lesueur area, and the second on the south coast stretching from the Stirling Range to the Fitzgerald River area (Speck 1958, Gibson *et al.* 1997). A number of Proteaceae genera clearly exhibit a bimodal heathland pattern of diversity (*e.g. Conospermum, Dryandra, Grevillea, Hakea, Isopogon* and *Petrophile*), while others (*e.g. Adenanthos, Banksia s.s.* and *Lambertia*) have their species richness concentrated in the southern heathlands (Speck 1958, Gibson *et al.* 1997). These kwongan communities are also characterised by their high levels of locally endemic species, with only 16% of 303 species of Proteaceae occurring in the two heathland centres found to be common to both (Speck 1958). The high levels of beta diversity displayed by SWAFR Proteaceae are emphasised in genera such as *Banksia s.s.*, where 48% of species are locally endemic habitat specialists (Cowling

& Lamont 1998). The patterns of distribution and endemism of species are closely tied to local geology, soil type and soil structure such that a diverse array of species can occur in close proximity where there are small differences in the underlying substrate (Butcher 2004). This is especially pronounced in the northern sandplain where, in the lateritic uplands around Mt Lesueur, the overall species composition of plots *c.* 1 km apart can vary by up to 60% (Hopkins & Griffin 1984).

The SWAFR endemic genus *Synaphea* R.Br. is undergoing taxonomic revision and currently comprises 51 named species (George 1995, Butcher 2000) and 12 undescribed taxa (Western Australian Herbarium 1998 onwards) in addition to numerous unclassified collections, many of which may be resolved as discrete taxa with further study. The taxa within *Synaphea* display high levels of regional endemism and this is reflected in the large number of conservation listed species (Western Australian Herbarium 1998 onwards, Atkins 2005). Examples of locally endemic and geographically restricted taxa from the northern sandplain include *S. recurva* A.S.George, *S. spinulosa* (Burm.f.)Merr. subsp. *borealis* A.S.George, *S. aephynsa* A.S.George (Priority 3), *S. lesueurensis* A.S.George (Priority 2), *S. endothrix* A.S.George (Priority 2), *S. oulopha* A.S.George (Priority 1) and *S. xela* R.Butcher, the new species described in this paper.

The close morphological similarity between the species of *Synaphea*, combined with their high level of regional specificity, has meant that many new species have been collected for the first time only recently. Putatively new taxa are frequently overlooked in the field through being mistaken for more common species or, if collected, are regarded as aberrant specimens of named species. *Synaphea xela* is one such species, first collected in 1993 by A.S. George during his preparation of the *Flora of Australia* treatment of the genus (1995) but subsequently unplaced due to a lack of corroborating collections. Further close examination of these specimens and additional fieldwork suggests this material

represents a distinct taxon. *Synaphea xela* is described here, prior to the completion of a full taxonomic revision of the genus, due to its apparent rarity.

Methods

This study is based on examination of herbarium collections (including types) from PERTH, supplemented by type material of an additional ten names from the collections of BM, K and MEL. Measurements of habit, stems and leaves were made from live material and herbarium specimens, with floral features measured from 70% ethanol preserved material and reconstituted flowers.

Taxonomy

Synaphea xela R.Butcher sp. nov.

Fruticulus expansus 0.1–0.4 m altus, c. 0.6 m latus. Petiolus 90–190 mm longus, glaber vel glabrescens. Folia e viridia caeruleis, glauca, 3-vel 4-plo trilobata, pinnatipartita, apicibus prominente mucronatis; lamina applanata vel undulata, secus nervum medium plicata. Inflorescentia 50–105 mm longa, circum folia aequantia vel eis longiora; pedunculi 50–210 mm longi, 1-3-plo ramosi, sparse appresse pubescenti; bracteae ovatae, 1–2.1 mm longae, glabrae. Perianthium glabrum; tepalum adaxiale curvatum, 4.9–5.7 mm longum, 2.2–2.7 mm latum, marginibus valde retrocurvatum; tepalum abaxiale 2.8–3.3 mm longum , 1.2–1.4 mm latum. Stigma ovatum vel quadratum, 0.8–0.95 mm longum, 0.9–1.3 mm latum; ovarium 1/2–3/4 inferiorius subtiliter sericeum vel pubescentium, trichomatibus apicalibus amplificatis ad basim angulatis. Fructus angustissime obovatus, 5–6.9 mm longus, 2.2–2.8 mm latus, sessilis, in rostrum breve apicale late conicum contractus.

T: *c.* 15 km NE of Eneabba [precise locality withheld for conservation purposes], W.A., 28 Aug. 1999, *R. Butcher RB 690*; holo: PERTH 07344058; iso: AD, CANB, K, MEL, NSW, NY.

Sprawling subshrub 0.1–0.4 m tall, c. 0.6 m wide. Numerous stems from base, 25–50 mm long, smooth, tight, grey-brown bark with longitudinal fissures, glabrous or with scattered appressed hairs, patches of dense, appressed hairs under and near leaf bases; internode stems 15–105 mm long, yellow-pink, glabrous to lightly appressed pubescent, lightly glaucous. *Petiole* 90–190 mm long, glabrous to glabrescent, few hairs at junction with sheath, lightly glaucous in grooves; sheath pinkish-light brown at margins, glabrous to glabrescent externally, tomentose to appressed densely silky internally. *Leaves* dull, dark blue-green, 3–4 x trilobed, pinnatipartite; ultimate lobes linear, oblong or broadly triangular, 2–11 mm long, 2–5.5 mm wide; apices acute, obtuse or rounded with prominent mucro, 0.8–1.7 mm long; lamina 40–85 mm long, 50–115 mm wide, glabrous, glaucous, concolorous; reticulation fine to moderate, shallow; stomatal guard cells prominent, +/- flush with epidermis; lamina flat to undulate, folded along midline, multiplanar, ultimate lobes gently concave; juvenile leaves bright red and pubescent; red with moderate to dense white pubescence, pinnatipartite. *Inflorescence* of terminal spikes, 50–105 mm long, c. equal to or shortly exceeding leaves, flowers moderately spaced, internodes 1.5–5 x flower length at base, 1/5–1 x flower length below lowest bud; peduncles green or green and red, 50–210 mm long, 1–3 x branched, sparsely appressed pubescent; basal sheath pink-red, 6–7.5 mm long, glabrous or with scattered hairs along midline and at apex externally, appressed silky along midline internally, margins ciliate; rachis green or green and red, glabrescent to sparsely pubescent at base, lightly pubescent at apex; bracts ovate, +/- horizontal to gently ascending, acute to obtuse, 1–2.1 mm long, glabrous with ciliate margin. *Perianth* curved horizontally to gently ascending, opening moderately to widely, glabrous; adaxial tepal strongly curved behind filament, 4.9–5.7 mm long, 2.2–2.7 mm wide, apex erect to hooded, margins strongly flared backwards, glabrous internally; abaxial tepal strongly convex, 2.8–3.3 mm long, 1.2–1.4 mm wide, the apex reflexed to 0.1–0.2 mm of length, hairs present behind anthers; lateral tepals gently falcate, 3.2–3.6 mm long, 2–2.7 mm wide, the apex reflexed to 0.2–0.6 mm of length, hairs present behind anthers. *Stigma* ovate to quadrate with slightly inrolled margins, broadly and shallowly emarginate to 0.1–0.2 mm of length, 0.8–0.95 mm long, 0.9–1.3 mm wide, +/- flat and reclining to concave in upper half ventrally. *Ovary* ovoid to obovoid with broadly conical beak to 0.2 mm long (after style separates), 1–1.2 mm long, 0.7–0.8 mm wide, finely silky to pubescent in lower 1/2 to 3/4, glabrous to sparsely pubescent at apex, beak glabrous to very sparsely puberulous, ring of 20–23 enlarged, translucent gland-like hairs at apex, hairs kinked at base then incurved over apex. *Fruit* very narrowly obovoid, smooth to very finely ribbed, 5–6.9 mm long, 2.2–2.8 mm wide, sessile, lightly pubescent in lower 1/2 to 3/4, glabrous to sparsely pubescent at apex, tapering evenly into a short, broadly conical, glabrous to sparsely puberulous beak (c. 0.2 mm long). *Seed* not seen. (Fig. 1 A–H)

Flowering. July–September. *Fruiting.* Fruits have been collected in August.

Specimens examined (6 of 6): WESTERN AUSTRALIA: *c.* 20 km NE of Jurien [precise locality withheld], 27 Aug. 1997 *R. Butcher & J.A. Wege RB 99* (UWA); 28 Aug. 1997 *R. Butcher & J.A. Wege RB 102* (PERTH); 28 Aug. 1999 *R. Butcher RB 689* (AD, CANB, K, MEL, PERTH); *c.* 15 km NE of Eneabba [precise locality withheld], 12 Aug. 1993 *A.S. George 17039* (BRI, DNA, HO, PERTH); *c.* 25 km ESE of Jurien [precise locality withheld], 13 Aug. 1993 *A.S. George 17049* (BM, NSW, PERTH).

Distribution. *Synaphea xela* has only been collected from north-east of Eneabba, on the edge of Wotto Nature Reserve, and from two small areas north-east and east-south-east of Jurien, on the edge of Mt Lesueur National Park (Fig. 2).

Habitat. The two areas where *Synaphea xela* occurs both have undulating topography but slightly different habitat. Near Eneabba the species grows in red-brown gravelly sand and loam over laterite, in kwongan heath comprising species of *Grevillea*, *Melaleuca*, *Hakea*, *Dampiera*, *Daviesia* and *Boronia*. Near Jurien the species grows in white-pink, grey-brown or brown clayey sand over laterite, in very open *Eucalyptus* woodland or heath abutting woodland, with species of *Hakea*, *Hibbertia*, *Comesperma*, *Daviesia*, *Gastrolobium*, *Mesomelaena*,
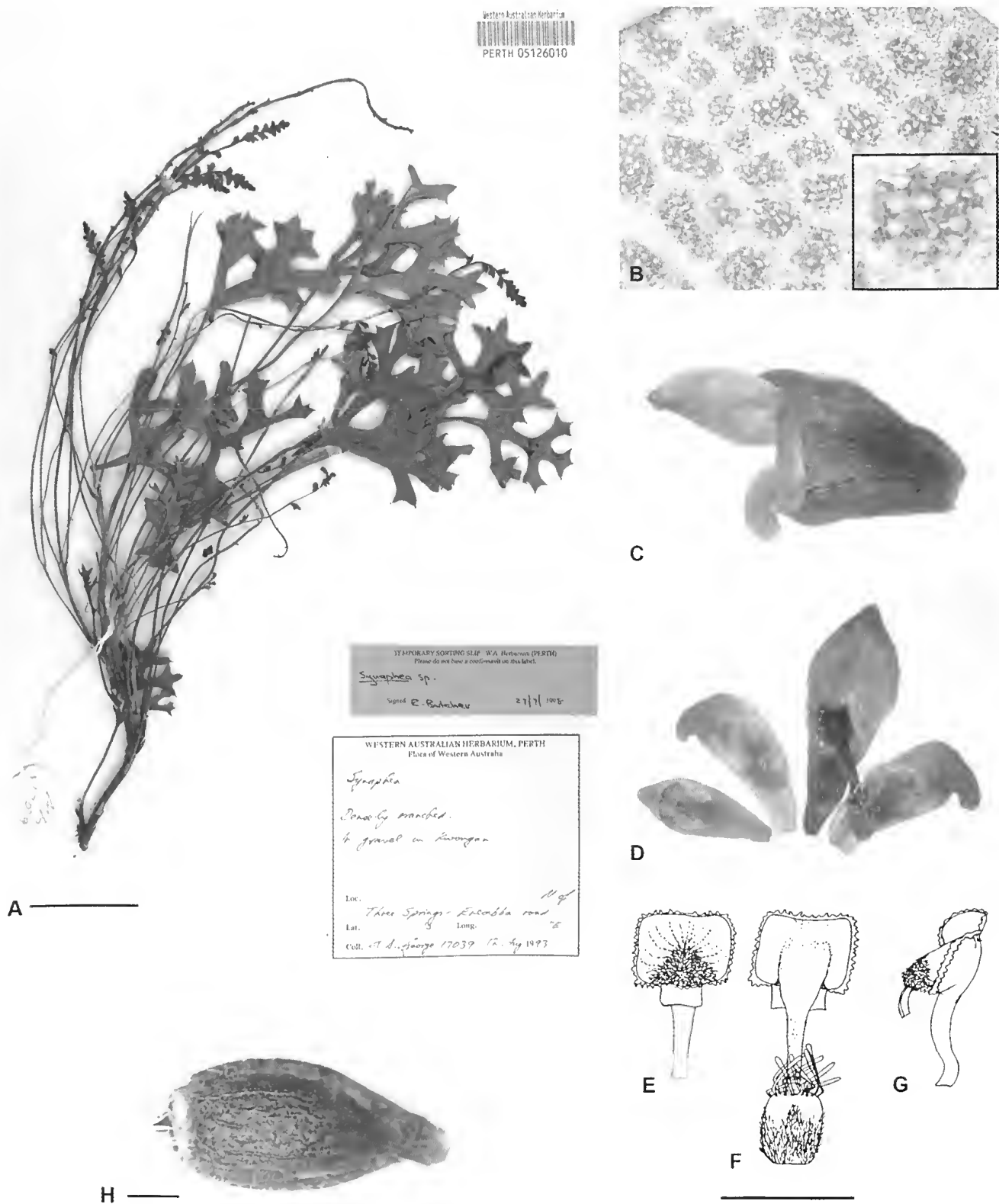
Figure 1. Images of *Synaphea xela*. A – Herbarium specimen; B – Leaf surface showing shallow reticulation and glaucous coat (inset – magnification showing stomatal guard cells +/- flush with the epidermis); C – Reconstituted flower showing floral shape and curvature of the lateral and adaxial tepal limbs and apices; D – Dissected reconstituted flower showing tepal shapes and gynoecium *in situ*; E – Ventral view of stigma showing the thickened, papillose lower half, gently concave upper half and fringing mucilage; F – Dorsal view of stigma showing the connection to the style and the ovary glabrous in the upper third with a ring of enlarged, kinked, apical trichomes; G – Lateral view of stigma showing the angled ventral surface and incurved margins; H – Fruit. A – D taken from *A.S. George 17039*, E – H taken from *R. Butcher RB 690*. Scale bar = 10 cm (A), 1 cm (B) and 1 mm (C – H).
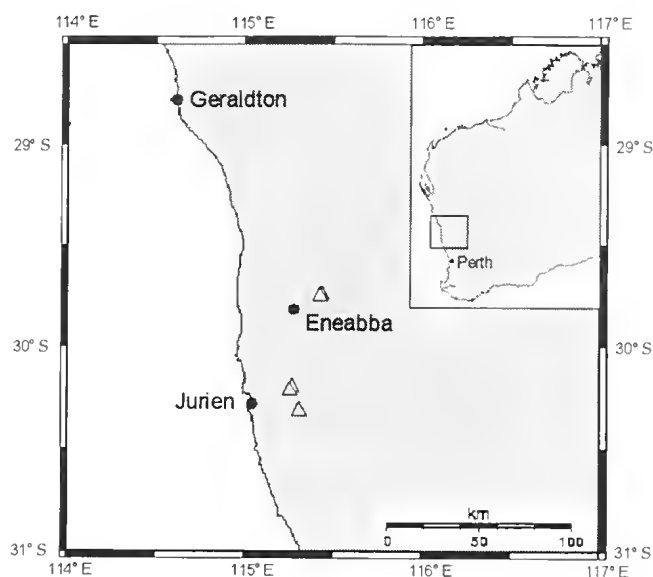
Figure 2. Distribution of *Synaphea xela* on the northern sandplain of south-west Western Australia.

Lambertia, Dampiera, Xanthorrhoea, Conospermum and *Thomasia.*

Etymology. This name of this species honours Alexander S. George for his significant contribution to the taxonomy of *Synaphea* and for his enthusiasm and support. In keeping with the nomenclatural tradition he started in *Synaphea* with *S. aephynsa* and *S. panhesya,* the epithet *xela* is an anagram of Alex.

Conservation status. A Priority 2 conservation code is considered appropriate for this species (CALM Conservation Codes for the Western Australian Flora, Atkins 2006). *Synaphea xela* is a very poorly known taxon which appears to be restricted geographically.

Affinities. Synaphea xela is distinctive among the species of *Synaphea* occurring on the northern sandplain in its combination of decumbent to sprawling habit, blue-green foliage, broad, shortly lobed leaves with long apical mucro, and its more-or-less quadrate, gently concave stigma with a broadly and shallowly emarginate apex.

Among the regional congeners, *Synaphea oulopha* is extremely distinctive in its clumped habit, highly divided, narrowly lobed leaves with very prominent reticulation, very small, openly spaced, dull yellow flowers, narrowly oblong stigma and the absence of apical trichomes on the ovary. Similarly, *S. endothrix* and *S. spinulosa* can be easily distinguished from *S. xela* by their erect habit, distinctly pubescent stems and peduncles, more densely arranged, puberulous to pubescent flowers and a more-or-less obovate stigma possessing broad, lateral lobes. *Synaphea aephynsa* is more similar to *S. xela* in its glabrous flowers and stigma morphology but is distinguished by its clumped to erect habit, yellow-green leaves with scarcely mucronate apices and less curved flowers with less reflexed margins and apices.

Some specimens of *Synaphea lesueurensis* and *S. xela* have similar leaf form; with narrowly obovate to oblanceolate ultimate leaf lobes, but *S. lesueurensis* has shorter petioles and lacks the prominent mucro seen in *S. xela. Synaphea lesueurensis* is also distinguished by its habit, in which the inflorescences are typically tangled through the leaves. Both of these species have widely opening flowers which are horizontally oriented, or gently ascending, in which the adaxial tepal is strongly curved behind the sterile filament, but *S. lesueurensis* has a prominently erect adaxial tepal apex and a stigma which is distinctly ovate with a small apical notch. *Synaphea quartzitica* is similar to *S. xela* in habit, leaf colour, prominently mucronate leaf apices, glabrous flowers and strongly reflexed adaxial tepal margins, but can be distinguished by its deeper, more angular leaf division, smaller flowers and narrowly oblong stigma.

Beyond the northern sandplain, *Synaphea xela* is similar in its habit to *S. damopsis, S. decumbens* and *Synaphea* sp. York (*F. Hort 666*), which are decumbent to sprawling taxa found in wandoo and/or jarrah woodlands of the Darling Plateau. *Synaphea damopsis* and *S. decumbens* can be distinguished from *S. xela* by their flat to undulate leaf lamina which is usually tapered into the petiole over a long distance, their pubescent perianth and bracts, as well as the sparse to dense wavy hairs on the rachis, peduncle, petiole and leaf lamina. These species are also distinctive in having an ovate stigma which is distinctly narrowed at the apex and strongly concave on the ventral surface. The stigma morphology of *Synaphea* sp. York (*F. Hort 666*) is similar to that of *S. xela,* but this taxon has larger abaxial tepals (4.4–5.1 mm long, 1.5–1.8 mm wide) and a larger stigma (1.2–1.3 mm long, 1.4–1.7 mm wide), and smaller (4.5–5.2 mm long), obovoid fruits.

Notes. This taxon was previously known as *Synaphea* sp. Eneabba (A.S. George 17039) on FloraBase (Western Australian Herbarium 1998 onwards).

The flowers of *Synaphea xela* tend to open tardily and many collections appear to have cleistogamous flowers, with fruits still developing on the plant.

Three unplaced *Synaphea* collections at PERTH (*A.S. George 16999, R. Butcher RB 438* and *R. Butcher RB 439*) from a single location alongside Carani West Road, east of New Norcia, are similar to *S. xela* in habit and leaf morphology but differ in their pubescent flowers and bracts, as well as a denser pubescence on the rachis and peduncle, a transversely oblong stigma with broad lateral lobes and the ovary pubescent throughout. These specimens may represent a distinct taxon allied to *S. xela,* but additional collections are required to confirm this.

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Holocene palynology of five wetland basins in the Becher Point area, southwestern Australia

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Abstract

The wetlands on the Becher Cuspate Foreland provide an opportunity to undertake palynological studies in a series of discrete small basins all belonging to the same wetland suite – the Becher Suite – from middle to late Holocene. The wetlands have formed progressively as the beachridge plain prograded westwards, and provide a landscape within a temporal framework wherein wetland initiation ranges from *circa* 4500 years in eastern locations to *circa* 900 years in western locations. Using patterns of surface pollen composition in relation to extant vegetation as a baseline the middle to late Holocene record was investigated in five wetlands, selected to incorporate different ages and plant/vegetation assemblages. The five wetland basins, in relatively close proximity and in the same climatic setting, have markedly different pollen history reflecting intra-basinal evolution. Pollen content of the sediment to shallow depth suggests that the following vegetation assemblages will be useful to interpret past vegetation patterns: *Centella asiatica* (L.) Urb. herb assemblage, *Baumea articulata* (R. Br.) S. T. Blake sedge assemblage, *Typha* (L.) sp. sedge assemblage, mixed *B. articulata* and *Typha* sp. sedge assemblage, *Melaleuca teretifolia* Endl. scrub assemblage, *M. rhaphiophylla* Schauer forest/shrub assemblage, with understorey of *C. asiatica*, *M. viminea* Lindley heath assemblage, *M. cuticularis* Labill. assemblage, and wetland margin of *Xanthorrhoea preissii* Endl., *Isolepis nodosa* (Rottb.) R. Br. and *Sporobolus virginicus* (L.) Kunth assemblages.

Radiometric dating of the sediment cores was used to provide an age structure. Pollen diversity and abundance against this age structure indicated that, except for *X. preissii* and *I. nodosa*, most wetland species were present over the interval of 4500 years BP to the present in the middle to late Holocene. However, there were a number of other important patterns in the down profile abundance of wetland pollen taxa and their inter-basin variation at isochronous levels: a lack of continuity down profile for some species; fluctuations in numbers of pollen taxa that were continuous; lack of correlation in timing of the peak pollen numbers between separate basins; variable total composition at the same isochron level from wetland to wetland; variable total composition of wetland pollen at different ages within the same wetland; the association of pollen species with sediment types; increases and decreases of wetland margin pollen taxa in the down profile composition; and the recent appearance of *I. nodosa* and *X. preissii* within the last *circa* 1500 years. The patterns of pollen derived from wetland vegetation in individual wetlands suggest that the ancestral distribution and abundance of plant assemblages in the Becher wetlands was a function of intra-basin environmental changes caused by wetland evolution. In contrast, pollen derived from upland vegetation exhibited continuity down profile, suggesting that delivery of upland pollen has been largely consistent, though variable in abundance and composition from basin to basin, and being exogenic, it has not reflected (hydrochemical, edaphic or hydroperiod) environmental conditions within the wetlands.

The combination of slow rates of sedimentation and bioturbation have obliterated any potential fine scale sequencing of pollen, resulting in a pollen record which may contain a composite of up to several hundred years of mixed wet and dry climate assemblages, making it difficult to interpret detailed climate history. However, the appearance of *X. preissii* and *I. nodosa circa* 1500 years ago, coupled with a corresponding change in stratigraphy, probably signals a recent increase in rainfall.

Keywords: palynology, Holocene, wetlands, Becher Point, south western Australia

Introduction

The wetlands in the Becher Suite in southwestern Australia provide an opportunity to study the pollen record in Holocene basins using an approach unprecedented in Western Australia. The wetlands have developed on the Holocene Becher Cuspate Foreland (Searle *et al* 1988; C A Semeniuk 2006; and Fig. 1), and occur in inter-dune depressions or swales of this beachridge plain. As described by Searle *et al* (1988), the cuspate foreland consists of a series of parallel beachridges, which range in age in the region from *circa* 7000 years at its eastern part, progressively younging westwards to contemporary at its shore. In the Becher Point area, the age of the cuspate foreland ranges from *circa* 5000 years at its eastern part to contemporary at its shore. In response to the progradation of the coast westwards, there was a general and progressive development of inter-dunal (swale) wetlands on the beachridge landscape (C A Semeniuk 2006). Thus, formation of the Becher Suite wetlands on this westward-younging prograding coastal plain commenced *circa* 4500 years in eastern and older parts of the beachridge plain of the Becher Cuspate Foreland and have continued to form up to *circa* 680 years in the western younger parts.

In general, elsewhere on the Swan Coastal Plain, wetlands in a Pleistocene landscape (of Pleistocene quartz sand dunes and lithified calcareous coastal dunes; *cf* Semeniuk & Glassford 1989) have developed as the post-glacial rising sea level resulted in regionally rising ground water tables across the ancestral (precedent) Swan Coastal Plain. As rising water table levels stabilised to present positions, lowlands and depressions in the landscape close in elevation to the present water table became inundated or waterlogged, and wetlands came into existence, filling with peat, diatomite and calcilutite (Semeniuk & Semeniuk 2004; 2006). Essentially, most of these wetlands came into existence at around the same time, co-incident with the stabilisation of a rising sea-level, and stabilisation of a rising regional ground water table. The wetlands of the Becher Suite provide a contrast to this pattern in that they have come into existence as the landscape developed by progradation. As such, the array of younging landforms, and younging wetland basins on the cuspate foreland provide an opportunity to study the comparative palynology of wetland basins in the same setting and suite initiated at different times during the Holocene. The basins in their near-contemporary setting are in close proximity and thus provide indication of how diverse the palynological record can be at the local scale. The wetlands also are reasonably well documented in terms of stratigraphy, hydrochemistry, and age structure and hence provide indications of how the palynological record reflects sedimentary, hydrochemical and ecological history.

The approach of this study is somewhat different from most palynological studies, in that there is a focus on several wetland basins in a comparative manner locally, rather than using one wetland to characterise the region. The main objective of the study was to construct the history of vegetation in five selected wetlands that have a range of ages but a similarity of sedimentary fill. The data in this paper, together with the results of C A Semeniuk (2006) and C A Semeniuk *et al* (2006), can be used to determine whether climate or intra-basinal evolution explains changes in wetlands and their vegetation through time.

Study sites, materials and methods

Five age-graded wetlands were selected for detailed stratigraphic and palynological examination to investigate the pollen record over the middle to late Holocene on the Becher Cuspate Foreland, *viz.* wetlands notated as 161, 162, 163, 135, and 9–14 (Fig. 1). All the wetland basins are relatively small and oval, *i.e.*, generally < 50 m x 100 m. The bases for their selection are outlined below.

Wetlands 161, 162, 163 are located on the *circa* 4500 year isochron of the beachridge plain of the Becher Cuspate Foreland (Fig. 1), and represent three adjacent wetland basins, which differ in terms of their time of initiation and their history of filling. Wetland 161 was selected as it is the oldest wetland in the study with the greatest thickness of (accretionary) wetland fill, while 162 and 163 were selected because they lie adjacent to 161 and each wetland is colonised by different assemblages of plants. Wetland 135 was selected because it is situated on the 3000 year isochron of the beachridge plain, representing a middle age wetland basin; it has sufficient thickness of wetland fill, and is currently colonised by a plant assemblage not represented in the other wetlands. Wetland 9–14 was selected because it is situated on the 1500 year isochron of the beachridge plain, and represents one of the youngest of the wetland basins in the region; it has sufficient thickness of fill, and supports a single plant assemblage. Although all wetland basins have sedimentary fill of calcilutite, the progressive filling of the basins with sediment has resulted in different thickness and, consequently, varying hydrological and hydrochemical history. These factors have effected the serial evolution of the vegetation.

The centre of each of the selected wetlands was cored using a 10 cm diameter PVC tube to extract an intact core. The cores penetrated to a depth to intersect the basement Safety Bay Sand that underlies the wetland sedimentary fill. The cores were frozen within an hour of their retrieval and stored in a freezer at -30° C until ready for processing. Later, the cores were split longitudinally, photographed, and subsampled. One half of the core was sampled for pollen, and for sediment for ^{14}C analysis. Small samples of sediment were extracted for palynological processing from the core using a 1 cm diameter micro-corer at the sedimentary surface, then at 3–5 cm depth, and thereafter at 10 cm intervals. To provide an age structure for the pollen, *circa* 20 grams of carbonate mud was taken from selected depths and prepared for ^{14}C analysis (Fig. 2). This mud sample was wet-sieved through a 63 μm mesh to eliminate any sand grains (these potentially may be earlier Holocene, or even Pleistocene grains), and to separate all mud fractions from biogenic, or exogenic sand and rootlet material > 63 μm. The sieved mud was collected in a large clean container. Because it was important that only Holocene wetland biogenic carbonate mud was used for radiocarbon analyses, slurried samples of the mud after the first sieving were re-sieved through the 63 μm mesh.
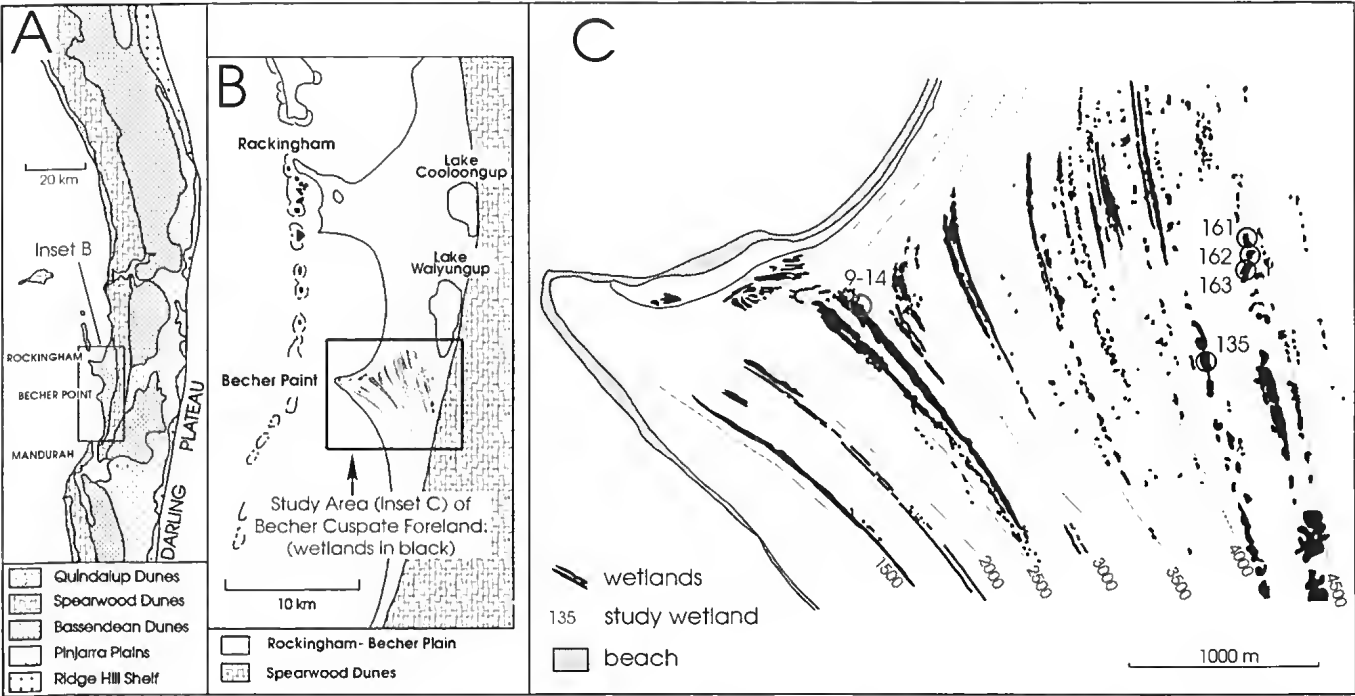
Figure 1. A. Location of Study Area in southwestern Australia. B. The Becher Point area and the Cuspate Foreland. C. Wetlands of the Becher Point area. Basins selected for study are circled and annotated; also showing isochrons in ^{14}C years (after Searle *et al*. 1988).
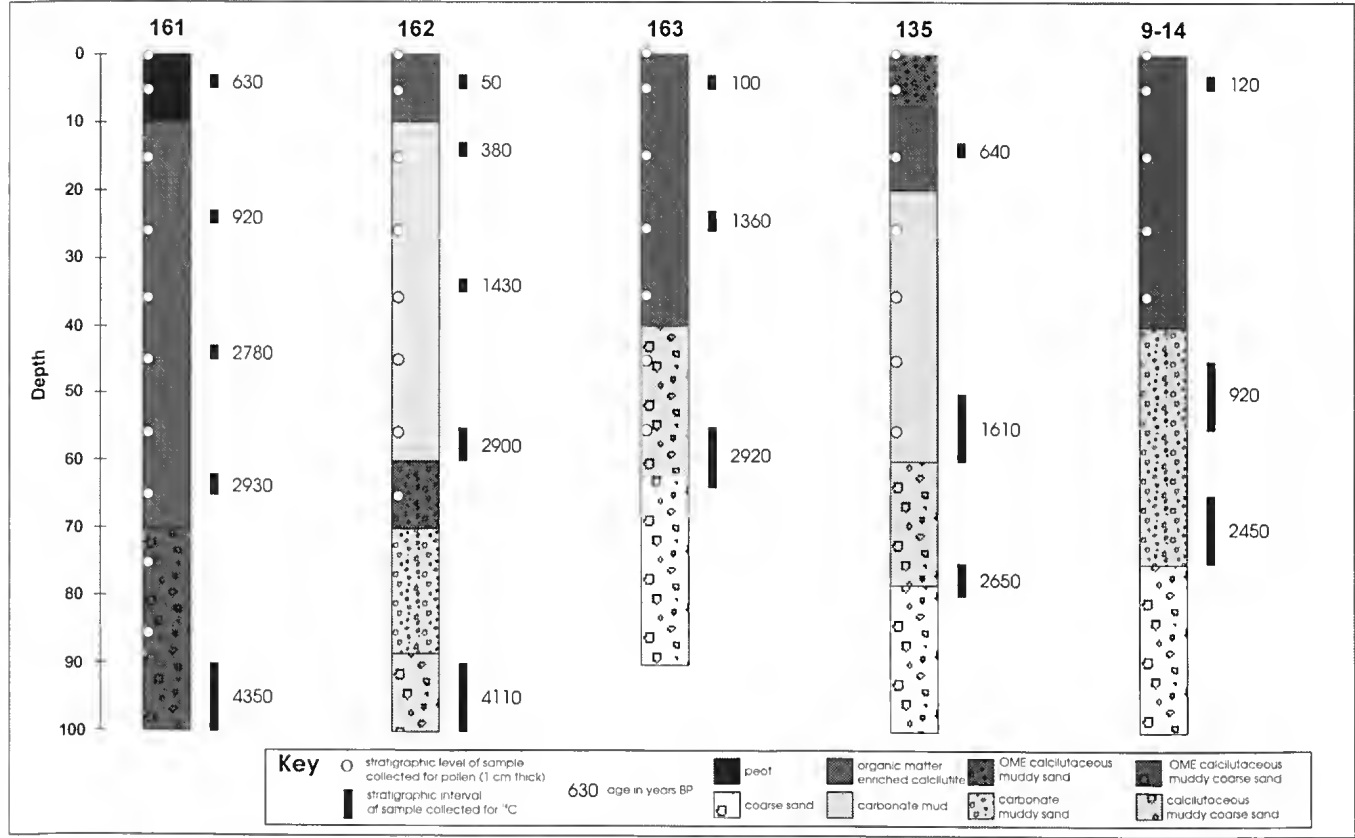
Figure 2. The stratigraphy of the centre of each of the wetland basins selected for study; also showing sampling points for pollen and samples collected for radiocarbon analyses. Sediment terms after Semeniuk & Semeniuk (2004). OME = organic matter enriched.

This second-stage sieved sample was then oven-dried in clean glass containers, and the base of the dried mud cake was examined with a stereoscopic microscope to ensure that there were no sand grains that could have preferentially settled to the base of the slurry. The dried sand-free mud was weighed to ensure that it conformed to the minimum required weight (18–20 g) for ^{14}C analysis. Samples were processed for ^{14}C at the CSIRO laboratories in Adelaide, South Australia, where they were acid-digested to collect CO_2 for the analysis using a

method for direct absorption of CO_2 for radiometric counting. A separate ^{13}C analysis of CO_2 was also undertaken for all samples.

Methods of pollen extraction and techniques of analysis are described in C A Semeniuk *et al.*, 2006. Sediment samples were processed to extract the organic material following the general procedures of Erdtman (1960), Phipps & Playford (1984) and Nilsson & Praglowski (1992). To determine the abundance of indigenous pollen species in each sample relative to a standard sediment volume, 1 cm^3 of each sediment sample was spiked with a known quantity of an alien pollen species (Betulaceae) prior to processing. Generally, a two hundred grain pollen count was conducted for each sample. Pollen identification was referred to modern pollen standards, referenced to publications, or assigned to an uncategorised group.

Pollen taxa identified by microscope were later assigned to the following groups:

1. wetland pollen;
2. upland pollen (*i.e.*, derived from the local beachridges);
3. regional pollen; and
4. uncategorised pollen.

Wetland pollen included all species of wetland plants occurring either in the wetlands or along the margins of the wetlands of the Becher Suite (as described by C A Semeniuk *et al* 2006). Upland pollen included only the species of plants occurring on the beachridges of the Becher Cuspate Foreland which had been identified in surface pollen samples. Similarly, regional pollen included only species identified in the surface pollen. Species outside of these groups were assigned to uncategorised pollen.

Numbers of natural pollen counted within samples were transformed to pollen per 1 cm^3 by multiplying them by the ratio of the known amount of betulid pollen seeded in 1 cm^3 of sediment to the betulid pollen counted in any sample. A mathematical problem potentially occurs for natural pollen taxa with zero frequency in the volume of sample prepared. In multiplying the actual numbers of natural pollen recorded by the ratio derived from the seeded betulid pollen, zero still remains zero in contrast to all other taxa which increase proportionately. Natural pollen recorded as zero in a low volume of sediment potentially may have been detected in low numbers if larger samples of sediment had been used, or truly may be absent even in larger sediment volumes. Although we recognise this problem, we consider that if natural pollen was recorded as zero in the pollen counts then that species was probably low in abundance (or absent) anyway.

Given the large range in numbers of grains of the pollen taxa in a cubic centimetre of sediment, two diagram formats have been used to illustrate their numbers and composition down profile and between sites. In the first instance, all numbers of pollen were transformed using betulid pollen as an internal standard to generate numbers of pollen grains in a cubic centimetre of sediment and plotted using a logarithmic scale. Marked variations in pollen numbers down-profile are smoothed out, so that this method of presentation

essentially shows absence/presence of all pollen down the profile and some broad measure of relative and comparative abundance for all species. In this context, small scale fluctuations in the graph represent abundance changes by factors, or by an order(s) of magnitude.

To highlight significantly abundant pollen numbers and to assist in the interpretation of the pollen record, a second method of presentation was used: only species with relatively higher frequencies of pollen per unit volume (*i.e.*, > 10^3 pollen grains per 1 cm^3, or > 3 on the logarithmic scale) were isolated and their abundance plotted arithmetically. In addition, so that pollen abundances could be readily compared at chronologically similar intervals, the stratigraphic columns were transformed so that they represent temporally evenly spaced sedimentary sections in 500-year increments.

A large number of radiometric dates in the Holocene wetland sedimentary sequences was available for this region (C A Semeniuk 2006), and so it was possible to determine mean rates of sediment accretion and assess/interpret the approximate location of the 500-year isochrons down the core profiles. Peaks in pollen numbers for the various species were correlated with radiocarbon dates of the sediments to facilitate inter-wetland comparisons. Where actual dates were not available, as described above, interpolated dates based on arithmetic proportioning of the sediment interval between two known dates were used. The stratigraphic columns in Figures 3, 4, 6, 7 & 8 thus illustrate the chronometrically partitioned sequences, the location of the pollen sampling sites against this chronometric adjusted framework, the location of the samples obtained for radiometric dating, and the abundance of the key species of pollen.

Background to the present palynological study, and stratigraphy of the wetland sites

Approximately 200 wetlands occur as basins in the inter-dune depressions of the Holocene beachridge plain in the Rockingham area (V & C Semeniuk Research Group 1991). Eighteen of these were studied in detail in terms of their landscape setting, stratigraphy, hydrology, hydrochemistry, and vegetation, (C A Semeniuk 2006) and 16 of this group were studied further by Semeniuk *et al* (2006) in terms of their pollen record in the surface sediment (as summarised below).

To provide a baseline for Holocene palynological studies for the Becher suite of wetlands from modern environments, *i.e.*, the pollen sources, the dispersion processes, pollen preservation, and palynological assemblages present in the surface sediments, the pollen assemblages in the surface sediments in the centre of 16 wetland basins in the Point Becher area were investigated by C A Semeniuk *et al* (2006). These authors (*op. cit.*) determined the ratio of wetland/upland species contributing to the surface pollen in each wetland, determined the contributions of local and regional pollen to the record, and identified indicator pollen assemblages to interpret fossil Holocene sequences. In the modern environment, the main wetland plant assemblages contributing to the pollen record included: 1. herblands of *Centella asiatica* (L.) Urb. in sumpland basin centres; 2. sedgelands of *Baumea articulata* (R. Br.) S. T. Blake in sumpland basin centres; 3. sedgelands of *Typha* (L.) spp.

in sumpland basin centres; 4. sedgelands of mixed *Baumea articulata* and *Typha* sp. in sumpland basin centres; 5. scrub of *Melaleuca teretifolia* Endl. in sumpland basin centres; 6. forest/shrubland of *Melaleuca rhaphiophylla* Schauer with understorey of *Centella asiatica* in centres or along margins of sumpland basins; 7. heath of *Melaleuca viminea* Lindley along sumpland basin margins; 8. stands of *Melaleuca cuticularis* Labill. in centres or along margins of sumpland basins; 9. fringing formations of *Xanthorrhoea preissii* Endl., with understorey of *Isolepis nodosa* (Rottb.) R. Br. and *Sporobolus virginicus* (L.) Kunth along sumpland and dampland basin margins; 10. sedgelands of *I. nodosa* along sumpland and dampland basin margins or in dampland basin centres; 11. grasslands of *Sporobolus virginicus* along sumpland and dampland basin margins; 12. mixed *I. nodosa* and *S. virginicus* along sumpland and dampland basin margins; 13. sedgelands of *Baumea juncea* (R. Br.) Palla along sumpland and dampland basin margins or in dampland basin centres; and 14. sedgelands of *Lepidosperma gladiatum* Labill. along sumpland and dampland basin margins.

The following key wetland plant species were commonly detected as pollen grains in the surface sediment in the 16 wetlands: *Baumea articulata, B. juncea, Centella asiatica, Isolepis nodosa, Lepidosperma gladiatum, Melaleuca cuticularis, M. viminea, M. rhaphiophylla, M. teretifolia, Sporobolus virginicus, Typha* spp. (as *T. domingensis* Pers. or *T. orientalis* C. Presl), and *Xanthorrhoea preissii*. C A

Semeniuk *et al* (2006) separated the pollen assemblages recovered from the surface sediments into six categories as related to extant vegetation: 1. that generated *in situ* from wetland basin vegetation; 2. that derived from *in situ* wetland margin vegetation; 3. that derived allochthonously from wetland vegetation; 4. that from ridge vegetation and transported to the wetland basin; 5. that from vegetation outside the region; and 6. unidentified pollen. Most of the surface pollen in the wetlands was derived locally from the local wetland and upland vegetation of the cuspate foreland. Generally, *in situ* wetland pollen constituted a reasonable proportion of the total pollen. Wetland margin pollen was abundant in only half the wetlands. Pollen from local beachridges was sub-dominant to pollen from wetland species in about half the wetlands, and dominant in the remainder. The contribution of regional pollen varied from low in most wetlands to relatively high numbers locally.

The modern potential dispersal mechanisms for pollen in this area are easterly and westerly winds, rain, insects, and avifauna, and local processes of *in situ* generation, sheet wash, and water transport. The differential effect of wind in transporting pollen was explored by C A Semeniuk *et al.* (2006) using local wetland species of *Melaleuca* as a signature, and the occurrence of upland species and regional, such as Casuarinaceae spp., *Olearia axillaris* (DC.) F. Muell. ex Benth., and *Eucalyptus marginata* Donn ex Smith pollen. The patterns show that delivery of pollen to the modern surface sediments of the wetland basins is heterogeneous.

Table 1

Description of wetlands in this study in terms of location relative to age structure, local geomorphic setting, wetland type, sedimentary fill, and vegetation

Wetland	Age Setting	Local geomorphic setting	Wetland type	Sediment fill	Extant vegetation (structurally, and numerically dominant species)
161	oldest, eastern part of suite; age of base of sedimentary fill is mid Holocene, *circa* 4300 ^{14}C years	relatively high beachridges border east and west margins	sumpland	incipient peat at surface and underlain by calcilutite, and basal calcilutaceous muddy sand	*Baumea articulata*
162	oldest eastern part of suite; age of base of sedimentary fill is mid Holocene, *circa* 4100 ^{14}C years	relatively high beachridges border east and west margins	sumpland	calcilutite, and basal calcilutaceous muddy sand	*Melaleuca teretifolia*
163	younger wetland in eastern part of suite; age of base of sedimentary fill is mid-late Holocene, *circa* 2900 ^{14}C years	relatively high beachridges border east and west margins	sumpland	calcilutite, and basal calcilutaceous muddy sand	*Juncus kraussii*
135	middle part of suite; age of base of sedimentary fill is mid-late Holocene, *circa* 2600 ^{14}C years	relatively high beachridge borders east margin; low beachridge on west margin	sumpland	calcilutite, and basal calcilutaceous muddy sand	*Melaleuca rhaphiophylla, Centella asiatica*
9–14	western part of suite; age of base of sedimentary fill is mid-late Holocene, *circa* 2400 ^{14}C years	low beachridges border east and west margins	sumpland	calcilutite, and basal calcilutaceous muddy sand	*Juncus kraussii*

The stratigraphy of the 5 wetlands selected for palynological study and location of samples for radiometric dating in the cores are shown in Figure 2. The setting of these wetlands is described in Table 1. Sediment terms are after Semeniuk & Semeniuk (2004)

The use of surface and near surface pollen assemblages as a baseline for interpreting fossil wetland pollen sequences

Description and interpretation of the pollen records for the near surface sediments in relation to extant vegetation in wetlands 161, 162, 163, 135 and 9–14 are provided in Tables 2 to 6. Given that there is vertical mixing, the pollen record in the surface and near-surface sediment (*i.e.,* the immediate surface sediment < 1 cm depth, 3–5 cm depth, and 10 cm depth) was noted against the extant wetland vegetation for a given wetland basin to be able to discriminate between the combined effects of *in situ* pollen production, import from other areas by wind, and contribution by vertical mixing (bioturbation). If a species was represented in the surface and near surface pollen but not present in the extant wetland vegetation for a given basin, note was then made of the likely source of pollen from other proximal and distal wetlands. The occurrence of particular pollen species in surface and near surface sediment when that plant species is absent in the wetland may be explained by 1) transportation into the basin by wind, 2) a sub-recent occurrence in the basin, or 3) bioturbation into the surface layers from depths > 10 cm.

The pollen data have been reduced so that only the most abundant species for any sample are presented, and the species at any sampling interval are ordered in terms of their abundance. The analyses of relative pollen abundance in the Tables 2–6 are presented in terms of

the relative stratigraphic sequence of surface (0–2 cm), near surface (3–5 cm), and at 10 cm depth, without any connotation as to absolute ages.

From the analyses in Tables 2–6, it is concluded that the following vegetation assemblages and their marginal components will be reflected in the pollen record, and can be used to interpret past vegetation patterns:

1. *C. asiatica* herb assemblage
2. *B. articulata* sedge assemblage
3. *Typha* sp. sedge assemblage
4. mixed *B. articulata* and *Typha* sp. sedge assemblage
5. *M. teretifolia* scrub assemblage
6. *M. rhaphiophylla* forest/shrub assemblage, with understorey of *C. asiatica*
7. *M. viminea* heath assemblage
8. *M. cuticularis* assemblage
9. wetland margin of *X. preissii, I. nodosa* and *S. virginicus* assemblages.

Descriptions of patterns down profile for total wetland pollen and upland pollen

The description of the pollen down the stratigraphic profile is provided below as total pollen down the profile, and as the composition of this pollen in terms of wetland, upland, regional, and uncategorised, and specific patterns for a given species. When viewing the total numbers of pollen down the profile (Fig. 3), it is also important to note the relative proportion of wetland, upland, and regional pollen contributing to this record (Fig. 4).

In wetland 161, excluding the surface pollen, numbers
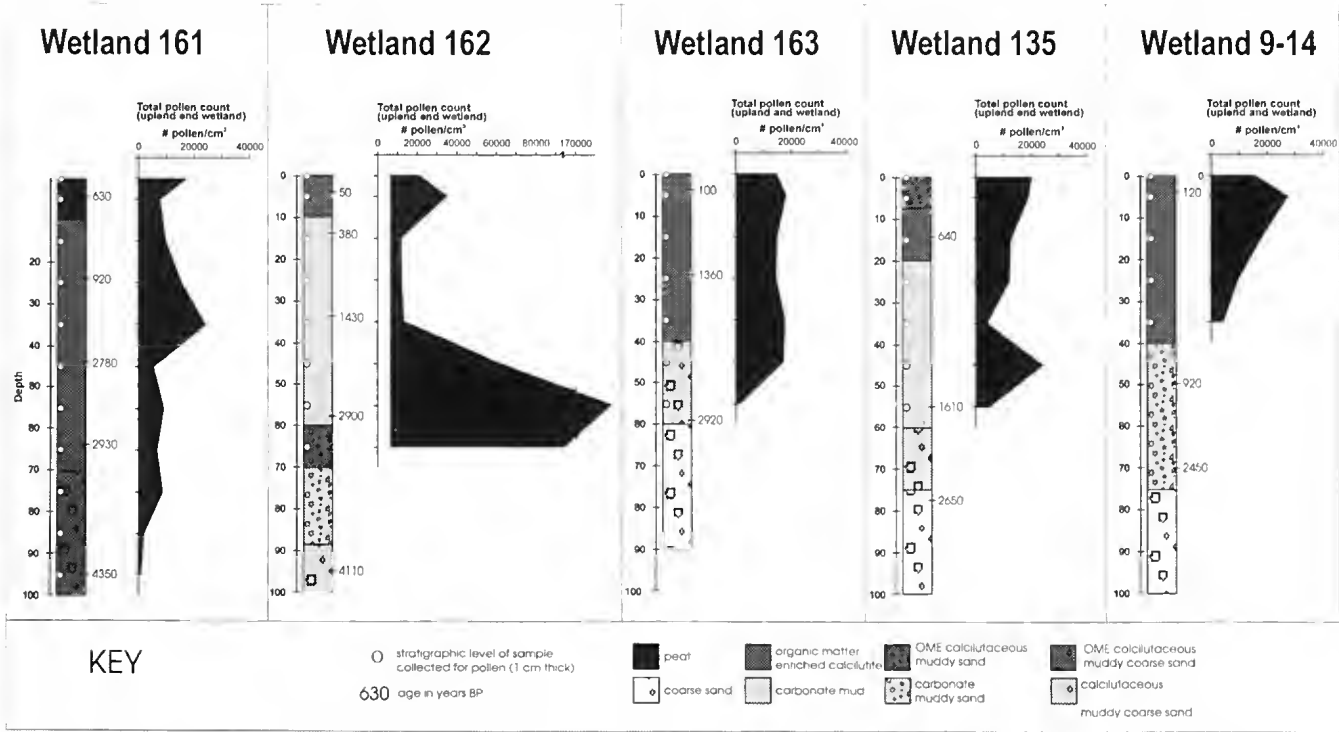
Figure 3. Total pollen down the stratigraphic profile for the five wetlands studied. The scale for pollen numbers is arithmetic.

Table 2

Wetland 161 – description and interpretation of the pollen record of surface and near-surface sediment in relation to intra-basinal extant vegetation, other proximal and distal wetland basins, and other physical processes

Wetland 161

Extant vegetation (most abundant species): *B. articulata*

Extant vegetation (less abundant, or on margins): *X. preissii, B. juncea, T. domingensis, T. orientalis, C. asiatica, S. virginicus*

Species occurrence (most abundant species):	Correlation of extant and fossil pollen	Extant plant taxa missing from record	Extra-basinal or sub-recent contribution	Comments
Pollen in surface sediment: *B. articulata, X. preissii, C. asiatica, Typha* sp.	contemporary record reflects dominant extant species, and *X. preissii* on margins	*B. juncea* (the species is too sparse in the modern vegetation); *S. virginicus*	*M. rhaphiophylla*	contemporary record suggests pollen reflects vegetation history; *M. rhaphiophylla* is a sub-recent component, or wind-derived; the nearest basins with this species are 135 and 136, from which pollen could be delivered via seabreezes
Pollen at 3–5 cm: *B. articulata, C. asiatica, Typha* sp., *X. preissii, S. virginicus*	pollen record reflects extant species, with more prominent contribution from margins	*B. juncea*	none	Fossil pollen suggests similar vegetation to present
Pollen at 10 cm: *B. articulata, C. asiatica, Typha* sp., *X. preissii, Triglochin* sp.	record reflects all extant species, with *Triglochin* mixed in from depth	*B. juncea*	none	Fossil pollen suggests similar vegetation to present

Table 3

Wetland 162 – description and interpretation of the pollen record of surface and near-surface sediment in relation to intra-basinal extant vegetation, other proximal and distal wetland basins, and other physical processes

Wetland 162

Extant vegetation (most abundant species): *M. teretifolia, C. asiatica, B. juncea*

Extant vegetation (less abundant, or on margins): *X. preissii, S. virginicus, I. nodosa*

Species occurrence (most abundant species):	Correlation of extant and fossil pollen	Extant plant taxa missing from record	Extra-basinal or sub- recent contribution	Comments
Pollen in surface sediment: *M. teretifolia, C. asiatica, X. preissii, B. juncea, M. rhaphiophylla, M. viminea, I. nodosa*	contemporary record reflects dominant extant species, and *X. preissii* on margins	*S. virginicus, I. nodosa*	*M. rhaphiophylla* and *M. viminea*	contemporary record suggests pollen reflects vegetation history; *M. rhaphiophylla* and *M. viminea* probably are sub-recent components, or wind derived; the nearest basins with these species are 135 and 136, from which pollen could be delivered via seabreezes
Pollen at 3–5 cm: *I. nodosa, X. preissii, C. asiatica, M. rhaphiophylla, B. juncea*	pollen record partly reflects extant species, with more prominent contribution from margins	*M. teretifolia,* indicating its absence from fossil vegetation assemblages at 5 cm depth	*M. rhaphiophylla*	fossil pollen suggests *M. rhaphiophylla* with broadly similar understorey to the present assemblage; the lack of *M. teretifolia* suggests that surface pollen has not been mixed down to 5 cm
Pollen at 10 cm: *B. juncea, M. rhaphiophylla, I. nodosa*	record reflects some extant species	*M. teretifolia, C. asiatica*	none	fossil pollen suggests *M. rhaphiophylla* with broadly similar understorey to the present assemblage; lack of *M. teretifolia* suggests no mixing of surface pollen to 10 cm

Table 4

Wetland 163 – description and interpretation of the pollen record of surface and near-surface sediment in relation to intra-basinal extant vegetation, other proximal and distal wetland basins, and other physical processes

Wetland 162
Extant vegetation (most abundant species): *J. kraussii, C. asiatica, B. juncea*
Extant vegetation (less abundant, or on margins): *X. preissii, S. virginicus, I. nodosa, M. teretifolia*

Species occurrence (most abundant species):	Correlation of extant and fossil pollen	Extant plant taxa missing from record	Extra-basinal or sub- recent contribution	Comments
Pollen in surface sediment: *I. nodosa, C. asiatica, S. virginicus, B. juncea, X. preissii, M. rhaphiophylla*	contemporary record reflects minor components of extant species and extant assemblages, and dominantly from the margins	*J. kraussii* (because of its poor preservation)	*M. rhaphiophylla M. teretifolia* (the latter is too sparse in the modern vegetation)	leaving aside *J. kraussii*, the contemporary record suggests pollen reflects vegetation history, with *M. rhaphiophylla* and *M. teretifolia* as a sub-recent component
Pollen at 3–5 cm: *C. asiatica, I. nodosa, S. virginicus, B. articulata, X. preissii*	pollen record largely reflects extant species, with more prominent contribution from margins	*J. kraussii* (because of its poor preservation)	*B. articulata*	fossil pollen suggests vegetation was *C. asiatica – B. articulata* dominated; the possibility that *B. articulata* is exogenic is rejected because the nearest basin (161) with this species is in the wrong direction for wind delivery, and the intervening basin (162) is devoid of its pollen
Pollen at 10 cm: *C. asiatica, S. virginicus, M. viminea*	record reflects some extant species	*J. kraussii* (because of its poor preservation), *B. juncea, X. preissii, S. virginicus, I. nodosa, M. teretifolia*	*M. viminea*	fossil pollen suggests vegetation was *C. asiatica – M. viminea* dominated with contributions from the margin by *I. nodosa* and *S. virginicus*

Table 5

Wetland 135 – description and interpretation of the pollen record of surface and near-surface sediment in relation to intra-basinal extant vegetation, other proximal and distal wetland basins, and other physical processes

Wetland 135
Extant vegetation (most abundant species): *M. rhaphiophylla, C. asiatica, J. kraussii, B juncea*
Extant vegetation (less abundant, or on margins): *X. preissii, S. virginicus, I. nodosa*

Species occurrence (most abundant species):	Correlation of extant and fossil pollen	Extant plant taxa missing from record	Extra-basinal or sub-recent contribution	Comments
Pollen in surface sediment: *S. virginicus, M. rhaphiophylla, I. nodosa, M. viminea, B. juncea*	contemporary record reflects extant species	*J. kraussii, C. asiatica* and *X. preissii*	*M. viminea*	leaving aside *J. kraussii*, contemporary record suggests pollen partly reflects vegetation history; *C. asiatica* has recently returned to this wetland; *M. viminea* is a sub-recent component, or wind derived, with the source as wetland 9–11
Pollen at 3–5 cm: *I. nodosa, M. cuticularis, M. rhaphiophylla, S. virginicus, X. preissii*	pollen record only partly reflects extant species	*J. kraussii, C. asiatica*	*M. cuticularis*	pollen suggests vegetation was *M. rhaphiophylla* dominated; *M. cuticularis* may be exogenic, but being in only a specific horizon suggests *in situ* accumulation
Pollen at 10 cm: *C. asiatica, X. preissii, M. viminea, S. virginicus*	record reflects extant species	*J. kraussii*	none	fossil pollen suggests vegetation was *C. asiatica – M. viminea* dominated, with contributions from margins by *X. preissii* and *S. virginicus*

Table 6

Wetland 9–14 – description and interpretation of the pollen record of surface and near-surface sediment in relation to intra-basinal extant vegetation, other proximal and distal wetland basins, and other physical processes

Wetland 9–14
Extant vegetation (most abundant species): *J. kraussii*
Extant vegetation (less abundant, or on margins): *C. asiatica, X. preissii, S. virginicus, I. nodosa, M. viminea*

| Species occurrence (most abundant species):	Correlation of extant and fossil pollen	Extant plant taxa missing from record	Extra-basinal or sub- recent contribution	Comments
Pollen in surface sediment: *M. viminea, S. virginicus, I. nodosa, C. asiatica, X. preissii*	contemporary record does not reflect extant species	*J. kraussii*	*M. viminea, X. preissii*	leaving aside *J. kraussii*, contemporary record suggests pollen will reflect vegetation history
Pollen at 3–5 cm: *I. nodosa, Typha* sp.	pollen record does not reflects central basin extant species, but only margin species	*J. kraussii, C. asiatica*	*Typha* sp.	fossil pollen suggests vegetation was *Typha* sp.
Pollen at 10 cm: *I. nodosa, C. cuticularis*	record reflects only one extant species of the margins	*J. kraussii*	*M. cuticularis*	fossil pollen gives no clear indication of vegetation composition; *M. cuticularis* may be *in situ*, or wind transported, and it is difficult to separate the two
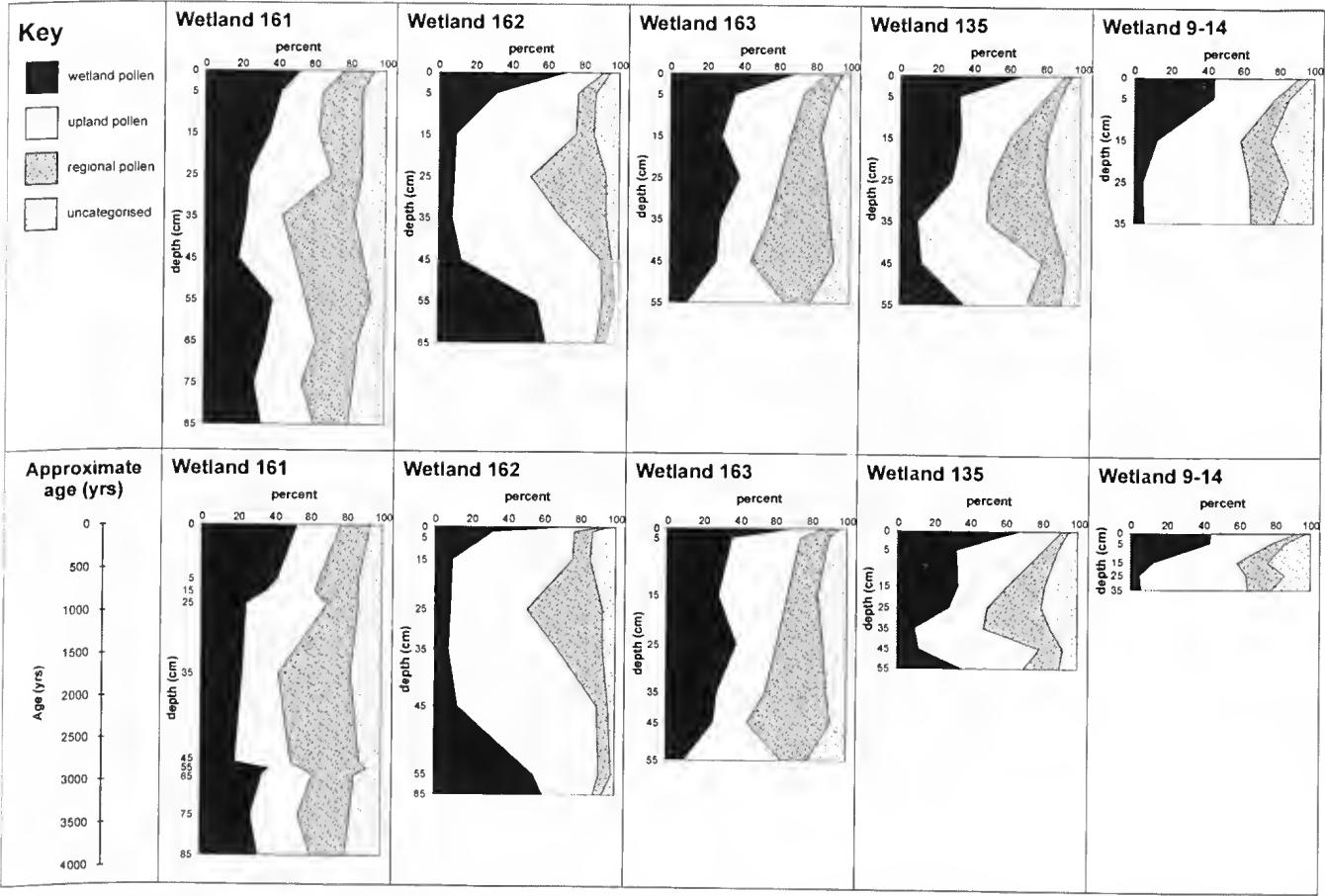
Figure 4. Graphs showing the composition of the pollen down the stratigraphic profile in terms of wetland pollen, (local) upland pollen, regional pollen and uncategorised pollen. The upper part of the diagram presents the data at true depth from the surface; the lower part represents the data on a chronometrically adjusted scale.

of pollen down profile increased to 35 cm then decreased at 45 cm and decreased again at 85 cm (Fig. 3). The highest values at 35 cm occurred as a result of general increases in subequal amounts in pollen from all categories, and particularly from regional pollen. In wetland 162, excluding the surface pollen, numbers of pollen down profile exhibited two peaks, a moderate one at 5 cm dominated by pollen from wetland and upland (ridge) species, and a large one at 55 cm, dominated by wetland species. In wetland 163, numbers of pollen down profile were fairly consistent to 45 cm, before falling sharply at 55 cm. In wetland 135, numbers of pollen down profile decreased from the surface to 35 cm, peaked at 45 cm, and decreased again at 55 cm. The higher numbers at 45 cm were due to upland pollen. The pollen numbers from wetland species down profile were low. In wetland 9-14, numbers of pollen down profile increased at 5 cm as a result of higher numbers of pollen from wetland and ridge species, then decreased.

Table 7

Total pollen numbers in each sediment type at different sites

Site and depth (cm)	Numbers of pollen/cm³	Sediment type, or soil
162–45	54,000	buried soil
162–55	181,000	buried soil
162–65	88,000	buried soil
162–5	28,000	organic matter enriched calcilutite (organic matter dominated, i.e., incipient peat)
161–5	7,500	organic matter enriched calcilutite
161–15	10,000	organic matter enriched calcilutite
161–25	15,000	organic matter enriched calcilutite
161–35	24,000	organic matter enriched calcilutite
163–5	18,000	organic matter enriched calcilutite
163–15	15,000	organic matter enriched calcilutite
163–25	14,000	organic matter enriched calcilutite
163–35	18,000	organic matter enriched calcilutite
163–45	17,000	organic matter enriched calcilutite
135–5	19,000	organic matter enriched calcilutite
9–14–5	27,000	organic matter enriched calcilutite
9–14–15	18,000	organic matter enriched calcilutite
135–15	12,000	organic matter enriched calcilutite and calcilutite
162–15	5,000	organic matter enriched calcilutite and calcilutite
161–45	5,000	calcilutite
161–55	9,000	calcilutite
161–65	6,500	calcilutite
161–75	8,500	calcilutite
161–85	2,000	calcilutite
162–25	5,000	calcilutite
162–35	6,000	calcilutite
135–25	12,000	calcilutite
135–35	4,000	calcilutite
135–45	28,000 (anomaly)	calcilutite
135–55	5,000	calcilutite
163–55	1,000	calcilutaceous muddy sand
161–95	1,000	calcilutaceous muddy sand
9–14–25	9,000	calcilutaceous muddy sand
9–14–35	4,000	calcilutaceous muddy sand

In absolute terms, the variation in pollen numbers with respect to sediment composition showed an interesting relationship. In Table 7, pollen numbers, ordered from highest to lowest, are shown to be related to groups of sediment types and buried soil. Pollen numbers in buried soils were highest, followed by incipient peat and organic matter enriched calcilutite (ranging from 10,000–24,000 pollen per cm³) which were also relatively consistent from site to site, both essentially reflecting high pollen production rates in wetlands with high plant production rates (culminating in the formation of peat and organic matter enriched calcilutite). Pollen numbers decreased in calcilutite (5,000–12,000 pollen per cm³) and in calcilutaceous muddy sand (1,000–9,000 pollen per cm³). The pollen numbers for sample 135–45 (calcilutite) were abnormally high, and are more characteristic of buried soils. At this site, high numbers of pollen from upland vegetation caused the marked increase in pollen abundance.

However, there were instances where the abundances of total pollen down profile also fluctuated within lithology, or did not markedly vary across some lithologic contacts (Fig. 3). The main peak in pollen abundance (24,000 pollen grains/cm³) down profile in wetland 161, for example, occurs within a lithologically homogeneous sequence of organic matter enriched calcilutite. The largest peak in pollen abundance (181,000 pollen grains/cm³) in wetland 162 occurs across a lithological boundary, being partly in organic matter enriched calcilutaceous muddy sand and partly in calcilutite. Generally in organic matter enriched calcilutite, pollen abundance is more or less uniform (± 15,000–20,000 pollen grains/cm³). The high peak in abundance (28,000 pollen grains/cm³) down profile in wetland 135 occurs in a distinct band within a lithologically homogenous sequence of calcilutite. The abundance of pollen grains in wetlands 9–14 decreases down the stratigraphic profile within a lithologically homogenous sequence of organic matter enriched calcilutite. In more detail, Figure 3 shows peaks in pollen abundance in wetland 161 occurring in calcilutite and organic matter enriched calcilutaceous muddy sand. In wetland 162 peaks occur in organic matter enriched calcilutite, calcilutite and a buried soil, in wetland 163 peaks occur in organic matter enriched calcilutite and calcilutaceous muddy sand, in wetland 135 peaks occur in calcilutite, and in wetland 9–14 peaks occur in organic matter enriched calcilutite.

The following wetland species, occurring in the central wetland habitats or wetland margin habitats, were sufficiently common and present in the samples for use in analyses in Figures 5–7: *B. articulata, B. juncea, C. asiatica, I. nodosa, L. gladiatum, M. cuticularis, M. rhaphiophylla, M. teretifolia, M. viminea, S. virginicus, Triglochin* sp, *Typha* spp (as *T. domingensis* or *T. orientalis), Xanthorrhoea preissii,* Cyperaceae spp. The following upland species, derived from local beachridges, or distally in the region, were sufficiently common and present in the samples for use in analyses in Figures 5–8: *Acacia cyclops* Cunn. ex Don, *Adriana quadripartita* (Labill.) Gaudich., Casuarinaceae sp., Chenopodiaceae sp 1, Chenopodiaceae sp 2, *Eucalyptus marginata,* Myrtaceae sp 1, *Olearis axillaris,* and *Stipa flavescens* Labill.
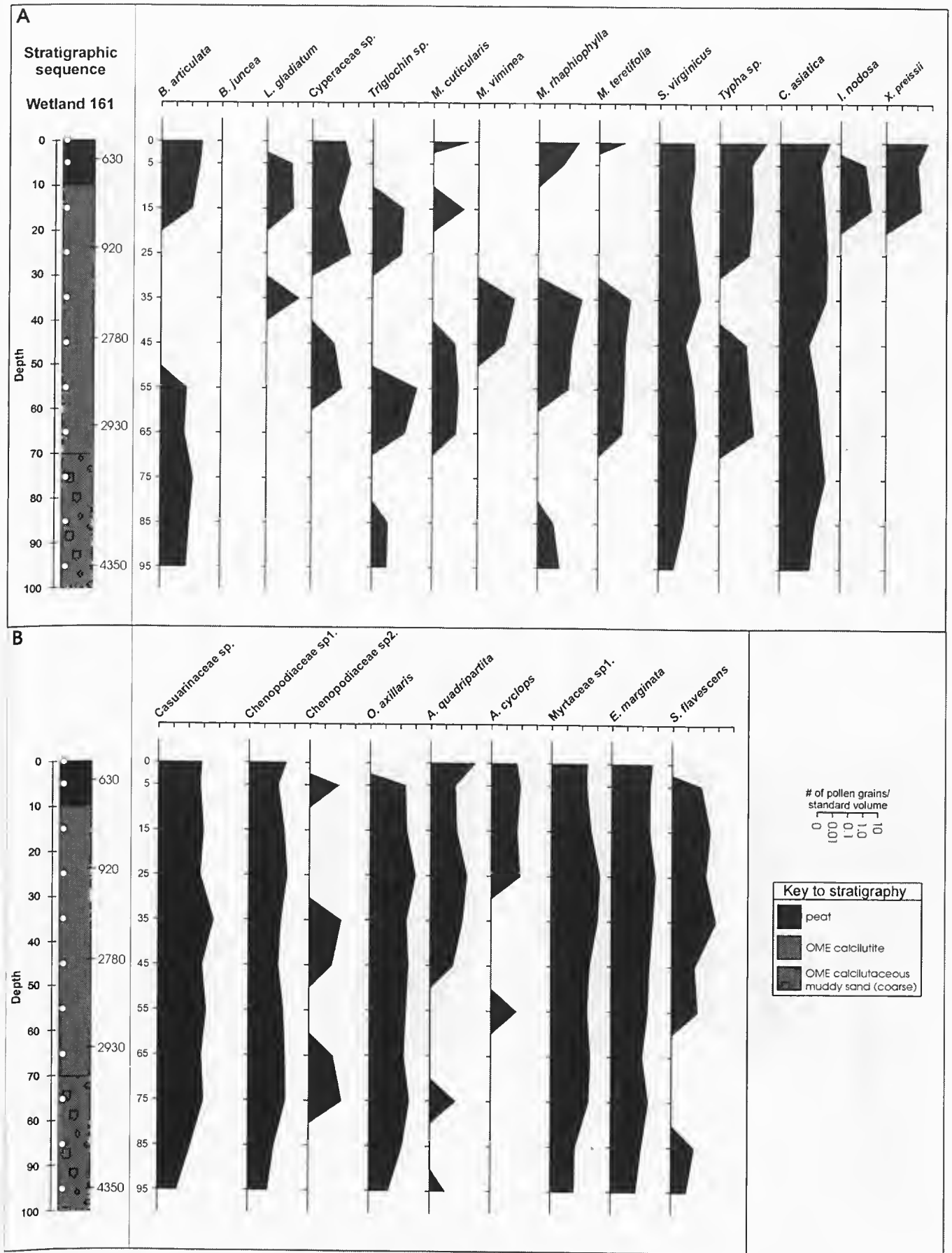
Figure 5. Graphs showing the composition of the various species of wetland pollen, upland pollen and regional pollen down the stratigraphic profile for each of the wetlands 161, 162, 163, 135, and 9–14. The upper part of each diagram (A) is of wetland pollen, the lower part (B) is of upland pollen and regional pollen. The scale for pollen numbers is logarithmic.
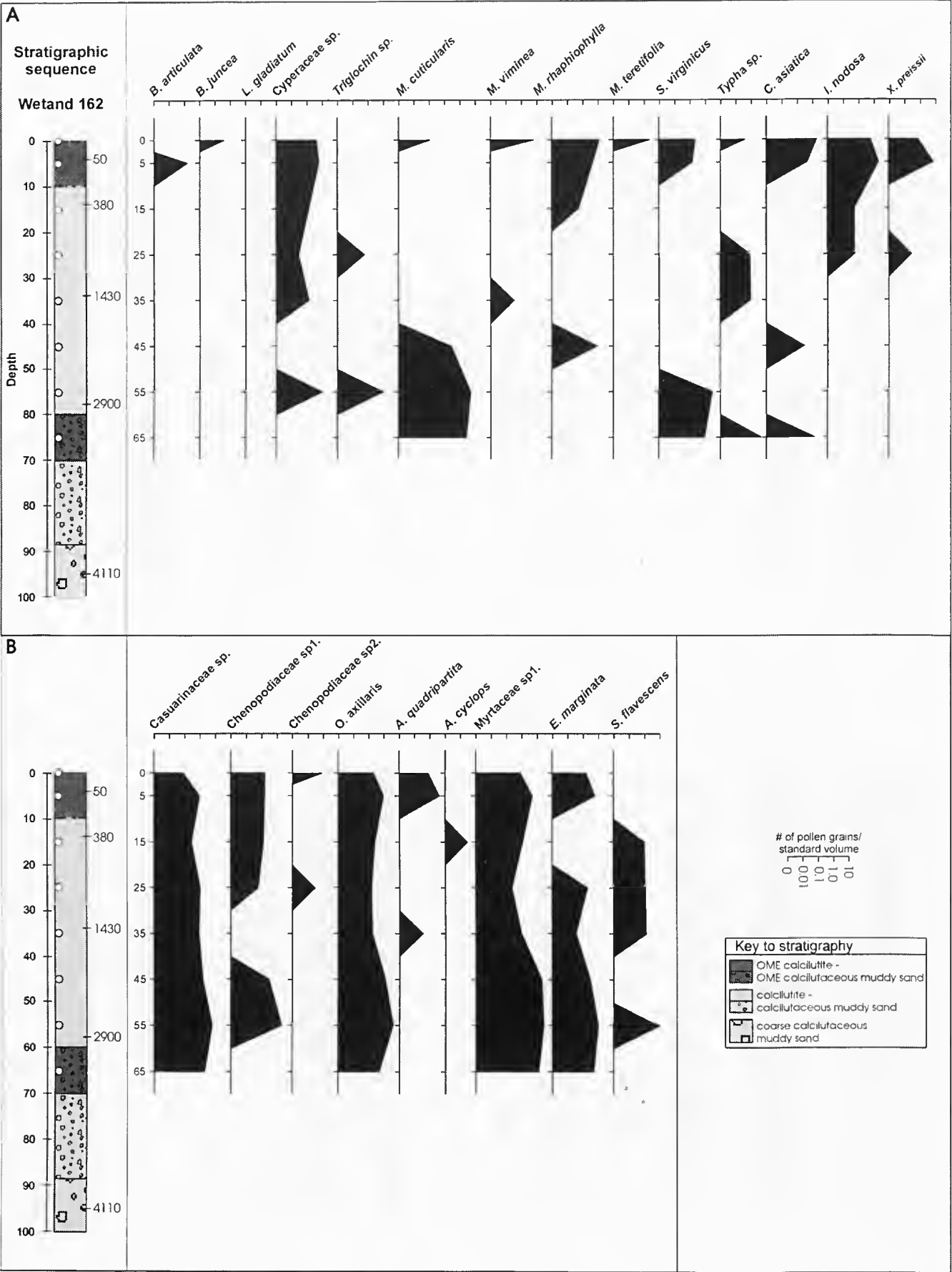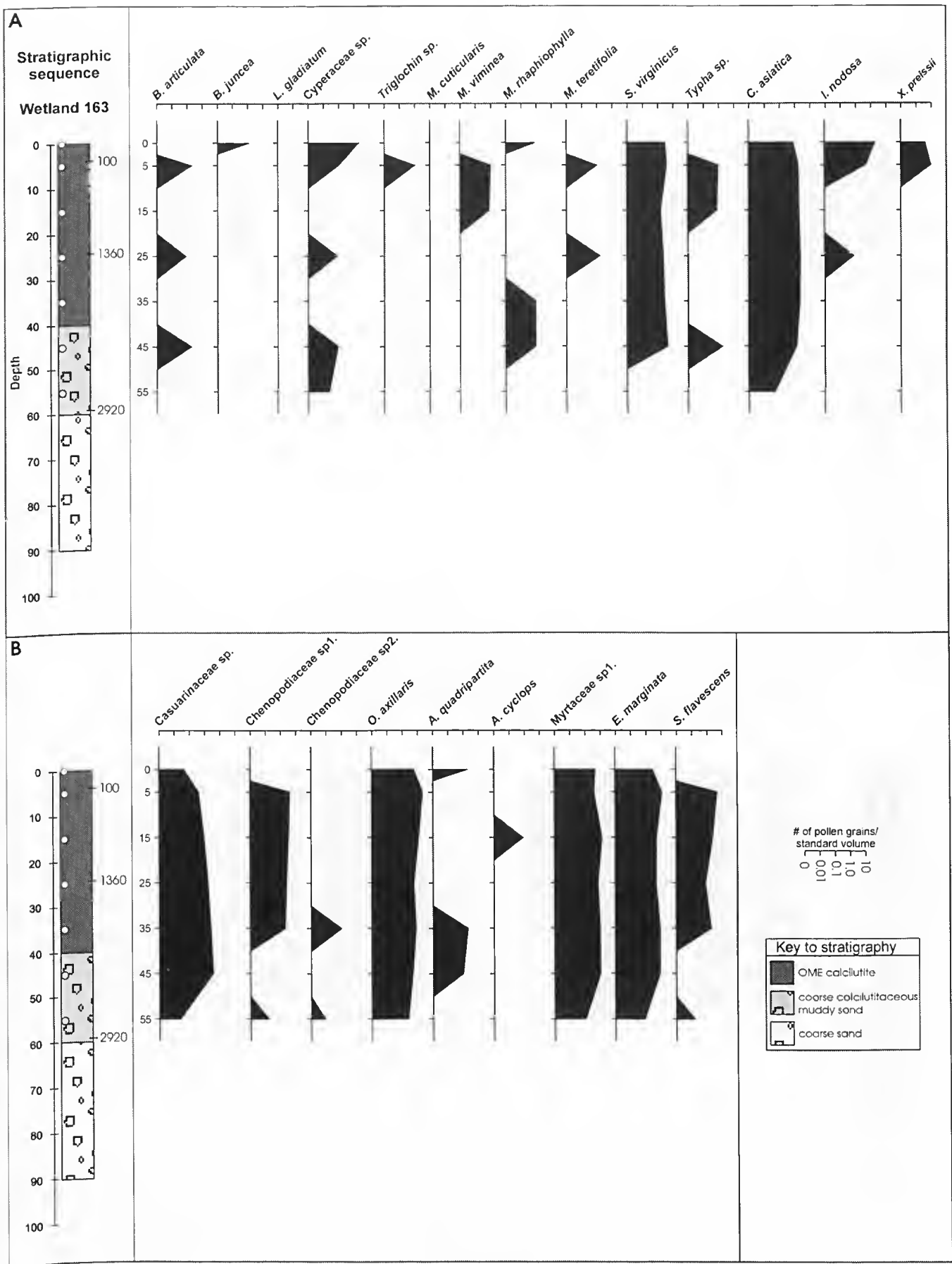
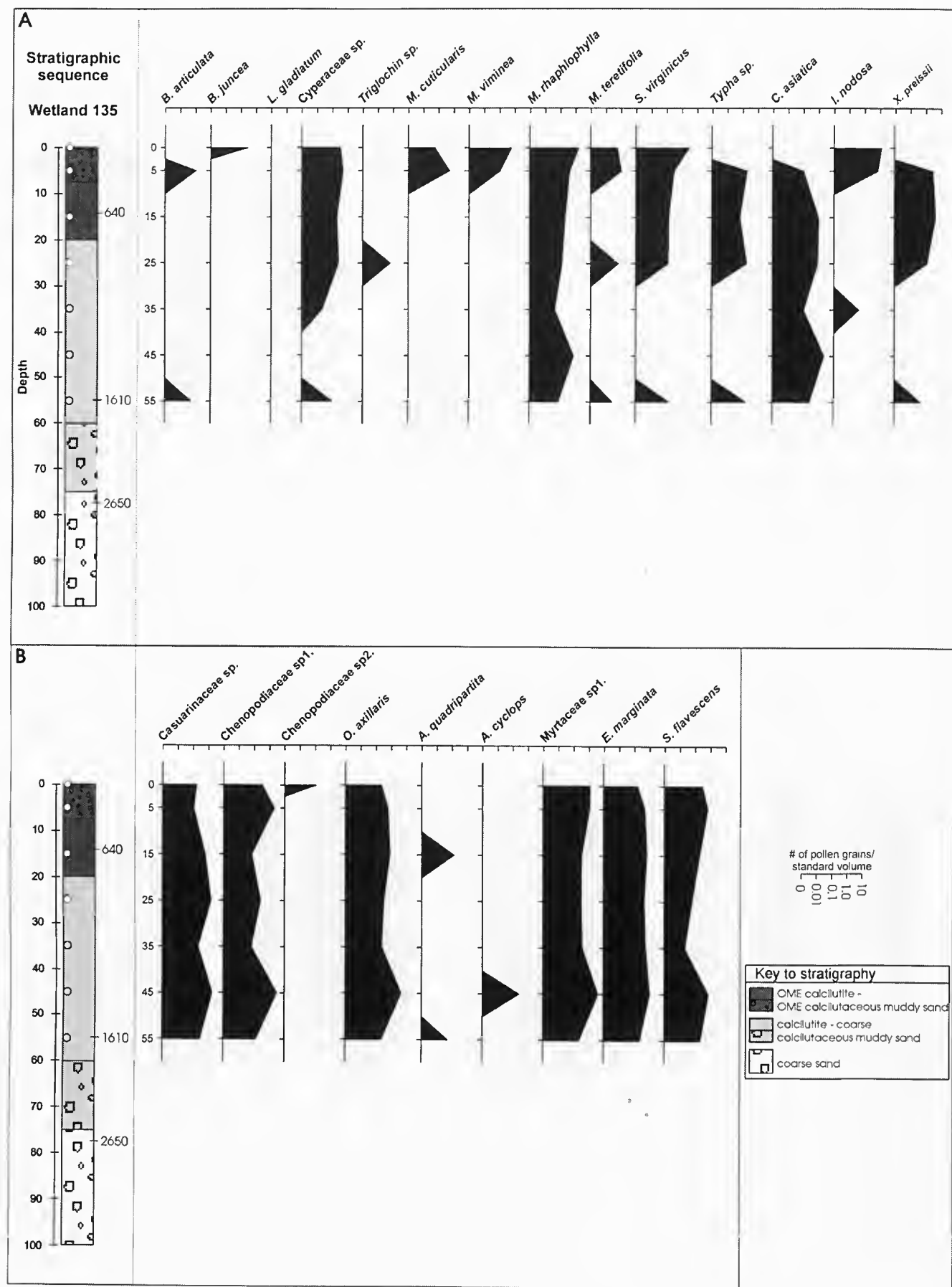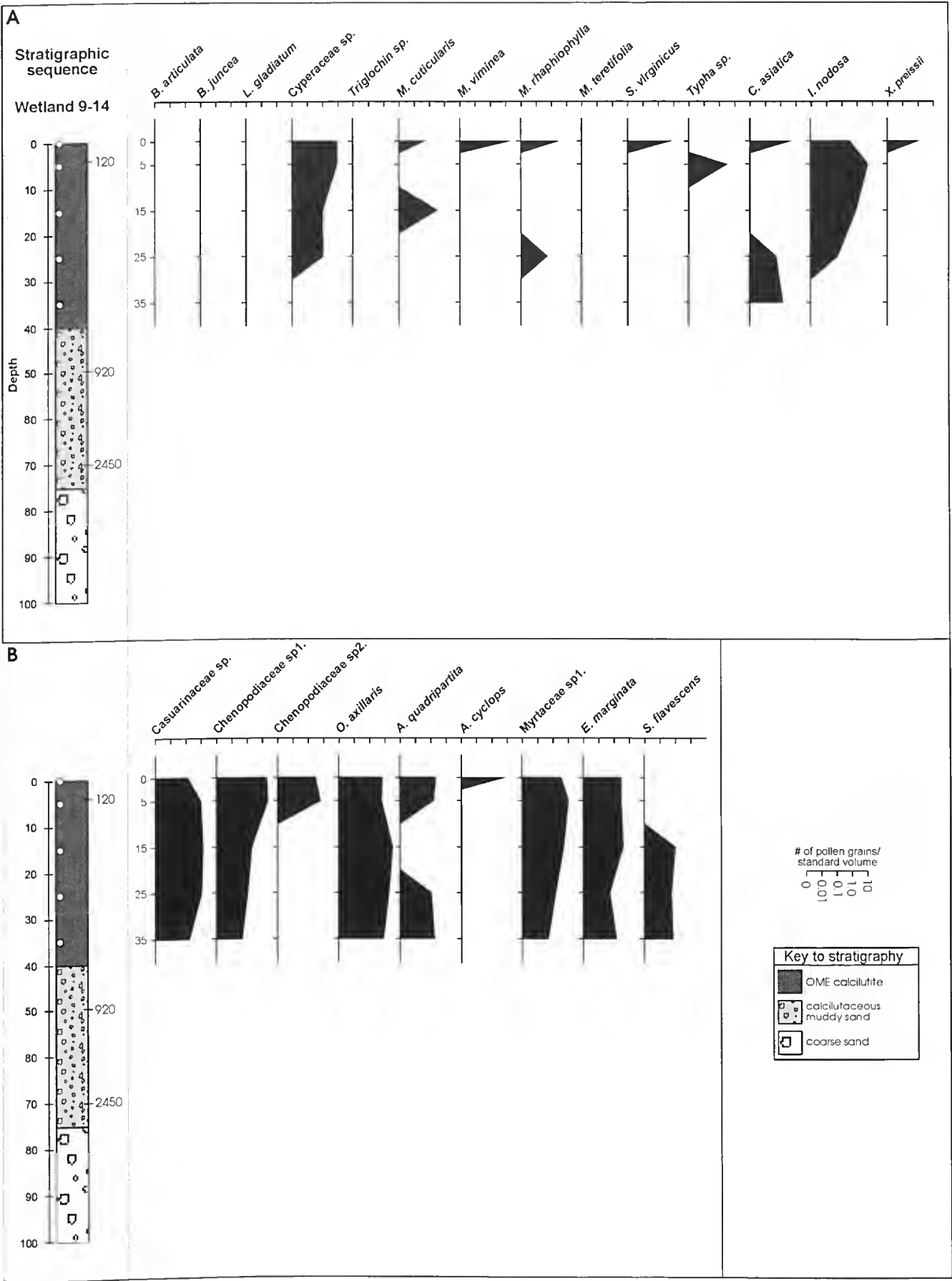Figure 5 (cont.)

Figure 5 (cont.)

141

Figure 5 (cont.)

Figure 5 (cont.)

In wetland 161, the wetland pollen numbers for individual species down profile were low. Two of the taxa were consistently present, *C. asiatica* and *S. virginicus*, the former whose numbers were in greater abundance, albeit fluctuating, and the latter, whose numbers were low and consistent. Of the other species which presently colonise the wetland, *B. articulata* was present in the surface layers and in minor amounts in the lower part of the profile, *L. gladiatum* was present to 35 cm, *X. preissii* to 15 cm, and *Typha* sp. to 65 cm (Fig. 5). The interval 35–65 cm was characterised by wetland species which are not extant in wetland 161, *i.e.*, *Melaleuca* spp. and *Triglochin* sp. From 0–15 cm and 55–85 cm, pollen derived from wetland species exceeded pollen derived from ridge species, the major families being Cyperaceae, Umbelliferae and Poaceae. Pollen derived predominantly from ridge species was relatively consistent down profile, with slight increases at 15, 25, and 35 cm, and a decrease at 95 cm. Pollen derived from regional vegetation increased at 25 and 35 cm.

In wetland 162, the wetland pollen numbers down profile ranged from high to low. None of the pollen taxa was continuously present. Of the species which presently colonise the wetland, *M. teretifolia* was present only in the surface layer, *C. asiatica* was present in the surface layer and exhibited a peak at 65 cm, and *X. preissii* did not occur below 25 cm (Fig. 5). The interval 15–45 cm was characterised by low numbers of wetland pollen, while the interval 45–65 cm, which exhibited the major peak, was characterised by species which do not currently occur in wetland 162, *i.e.*, species of *Melaleuca* other than *M. teretifolia*, and *Triglochin* sp. Pollen from ridge species and pollen derived from regional vegetation increased at 45 and 55 cm, paralleling the increase in total pollen numbers.

For individual species, in wetland 163, the wetland pollen numbers down profile were low and dominated by pollen from *C. asiatica*, *S. virginicus* and *C. asiatica*, which presently colonise the wetland, were consistently present throughout the profile and showed only minor fluctuation. Of the other species which presently colonise the wetland, no pollen of *J. kraussii* was found, Cyperaceae spp. (which potentially includes *B. juncea*) was present in the surface layers and in minor amounts in the lower part of the profile, and *X. preissii* did not occur below 5 cm (Fig. 5). Pollen from various ridge species did not show any consistent pattern down profile. Compositae displayed alternate increases and decreases down profile, while few pollen from Chenopodiaceae and Poaceae occurred below 35 cm. A slight increase in overall numbers of pollen from the ridges occurred at 35 cm. Pollen derived from regional vegetation increased at 45 cm.

In wetland 135, *M. rhaphiophylla* and *C. asiatica*, which colonise the wetland, were the only species consistently present throughout the sediment profile and both showed fluctuations. Of the other species which presently colonise the wetland, those of Cyperaceae were present in most layers, in minor amounts, *S. virginicus* was highest in the surface layer and decreased down profile, and *X. preissii* occurred between 5 and 25 cm and again at 55 cm (Fig. 5). The composition of the wetland pollen varied down the profile, with dominance by all four species of *Melaleuca* at the surface changing to dominance by *C. asiatica* and

M. rhaphiophylla at 45 cm. Except at the surface, pollen derived from species on the ridges exceeded wetland pollen, with a minor peak at 5 cm and a second higher peak at 45 cm comprising Chenopodiaceae, Compositae, and Poaceae. Pollen derived from regional vegetation increased at 45 cm.

For individual species, in wetland 9–14, the numbers of wetland pollen down profile were low. Pollen from Cyperaceae and *I. nodosa*, which currently colonise the wetland, were consistently present to 25 cm (Fig. 5). The patterns in these two taxa mirrored the overall population pattern. No pollen of *J. kraussii*, the species that currently dominates the wetlands, was found. Pollen from ridge species showed dissimilar frequency patterns down profile, Compositae pollen increased to 15 cm then decreased, while Chenopodiaceae pollen increased at 5 cm then remained consistent. A slight increase in pollen from the ridges occurred at 5 cm. Pollen derived from regional vegetation was relatively consistent down profile with a slight increase at 15 cm.

Patterns of species abundance down profile in relation to age structure

Pollen abundances down profile were graphed in relation to the ages determined for each core to construct the palynological history in individual wetlands, and in order to compare patterns in a single species across wetlands, in pollen categories, and in species associations within a framework of (reconstructed) temporally equivalent isochrons (Figs 6–8).

Palynology of individual wetlands with respect to selected species

Pollen abundance against age structure in wetland 161 (Figs 6A & 7A) indicates that the extant species, *i.e.*, *B. articulata* and *C. asiatica*, were present in the early stage of wetland development (4350 ^{14}C yrs BP), but that *X. preissii* is a relatively recent arrival (920 ^{14}C yrs BP to the present). The extant assemblages appear to have replaced sub-recent assemblages of *Melaleuca* species. The surface sediments (0-5 cm) in wetland 161 span over 600 years in contrast to the other wetlands in which the equivalent interval spans 100–200 years. This suggests that pollen species recorded in the surface layer of 161 are likely to be from a sequential series of plant assemblages, whereas in other wetlands the potential mixture of recent and sub-recent plant assemblages will be less. In wetland 162, the pollen record indicates that the extant species, *i.e.*, *M. teretifolia* and *X. preissii* are also relatively recent (< 1000 years), again having replaced other *Melaleuca* species (Figs 6B & 7B). The early plant assemblages contained *C. asiatica*, *Typha sp.*, *M. cuticularis*, and *S. virginicus*. The first two species are likely to be related to the buried soil horizon and the latter two species to the commencement of carbonate mud deposition. In wetland 163, the pollen record indicates that some of the extant species, *C. asiatica* and *S. virginicus*, were present from the time of wetland initiation up to the present, and others are relatively recent arrivals, *X. preissii* (Figs 6C & 7C). *Melaleuca* pollen occurs in the sub-recent. In wetland 135, the pollen record indicates that the extant species, *M. rhaphiophylla* and *C. asiatica*, were present near the beginning of

wetland development (Figs 6D & 7D), together with a number of other species. Pollen from several species of *Melaleuca* occurs in the sub-recent. For wetland 9–14, it is not possible to determine the colonisation period for *J. kraussii* (Figs 6E & 7E), but *C. asiatica* was again an early coloniser. Although the pollen from plants in the current wetland assemblages is present throughout the stratigraphic cores, the earliest record of the two marginal species, *I. nodosa* and *X. preissii*, in the Becher area is *circa* 1500 ^{14}C yrs BP.

Correlation between basins of patterns for selected pollen species in three pollen categories

The peaks in the down profile abundance of selected species drawn from three categories of pollen, *viz*., wetland, ridge, and wetland margin, were examined. The two wetland pollen species which were most consistent throughout the wetland cores, *C. asiatica* and *S. virginicus*, together with *M. rhaphiophylla*, *M. viminea* and *Triglochin* sp., were selected, and patterns were compared within each wetland basin and between wetlands. Pollen of three species deriving from upland vegetation were selected: Casuarinaceae, which would indicate aeolian transport from the east; *O. axillaris* which would indicate aeolian transport from the west; and *Stipa flavescens* which indicates aeolian transport or sheet wash input from local ridges. The third group consisted of species of plants which currently colonise the wetland margins and/or invade the wetlands during periods of below average rainfall, *X. preissii* and *Adriana quadripartita* (Labill.) Gaudich.

The peaks in pollen abundance down profile for selected wetland species, as distinct from total pollen numbers, did not relate to sediment type. For example, Figure 7A shows the peaks in abundance in *C. asiatica* in wetland 161 occurring in calcilutaceous muddy sand and in organic matter enriched calcilutite, whereas Figure 7D shows the peaks in abundance of the same species in wetland 135 to occur in organic matter enriched calcilutite and in calcilutite. For *M. cuticularis*, the peak in abundance crosses two lithologic types (organic matter enriched calcilutaceous muddy sand, and calcilutite).

There appears to be some co-incidence in timing of increased abundance of several wetland species within a wetland basin, *e.g.*, in wetland 161 there were concurrent peaks in four of the five selected wetland species, *C. asiatica*, *S. virginicus*, *M. rhaphiophylla* and *M. viminea* *circa* 1800 ^{14}C yrs BP. However, there was less agreement between basins, *e.g.*, *C. asiatica* showed peaks in wetlands 161 and 163 around 1800 ^{14}C yrs BP, but not in wetlands 162 or 135. Similarly, there was a peak in *S. virginicus* pollen in wetland 163 *circa* 2160 ^{14}C yrs BP which was not evident in any of the other wetlands.

There also appears to be some co-incidence in timing for increased abundance in pollen of upland species within a single basin, *e.g.*, in wetlands 135 and 162 there were concurrent peaks in the three species *circa* 1370 and 2900 ^{14}C yrs BP, respectively. There was only intermittent co-incidence in timing for increased abundance in pollen between wetlands, *e.g.*, peaks occurring at *circa* 2900 ^{14}C yrs BP in wetlands 162 and 163. The dates for peaks in wetland 9–14 suggest that the frequency of peaks may be greater if sampling was undertaken at a narrower interval.

The peaks in abundance down profile for the marginal species such as *I. nodosa*, *S. virginicus*, and *M. viminea*, were more frequent than either of the other two categories. There was some agreement between the timing of peaks in that, for many, there was a corresponding occurrence in at least one other wetland basin.

From the beginning of wetland development to the present, the species composition of both subregional (upland, beachridge) and regional pollen contribution is similar, but there have been changes in abundance. For example, in wetland 162, there was a 1000-year period in which Casuarinaceae pollen increased, reaching its maximum abundance *circa* 2900 ^{14}C yrs BP. This was briefly reflected in wetland 161, in which two additional increases in regional pollen occurred. In wetland 163, there was also a 1000 year period in which Casuarinaceae pollen increased, reaching its maximum abundance *circa* 2100 ^{14}C yrs BP. In wetland 135 peaks in numbers of Casuarinaceae pollen occurred *circa* 900 and 1400 ^{14}C yrs BP, and in wetland 9–14, a peak occurred recently.

Interpretation of results

As noted above, total pollen numbers varied with respect to sediment type and soils: pollen numbers were highest in buried soil horizons, followed by those in incipient peat and organic matter enriched calcilutite, which were also relatively consistent from site to site. Pollen numbers decreased in calcilutite and in calcilutaceous muddy sand. The abundance of wetland pollen in relation to sediment type and soils reflects the productivity of plant material (producing organic matter enriched substrates, incipient peats, and soils) which in turn results in increased production of *in situ* wetland pollen.

Down profile variation in abundance of wetland species pollen and inter-basin variation of these species at isochronous levels show several patterns:

- in some cores there is a lack of continuity in, but not the complete disappearance of pollen down profile for the majority of wetland plant species (*e.g.*, wetlands 161, 162 and 163 in Fig. 5);

- there are fluctuations in pollen species which are present throughout the profile (*e.g.*, *C asiatica* and *S. virginicus* in wetland 161 in Fig. 5; *M. rhaphiophylla* in wetland 135 in Fig. 5);

- there is a lack of correlation in timing of the peaks in pollen numbers between separate basins (*e.g.*, *M. teretifolia*, *M. rhaphiophylla* and *M. cuticularis* in wetlands 161, 162, 163, 135 and 9–14 in Fig. 5);

- the total composition of wetland pollen from wetland to wetland at the same isochron level varies;

- the total composition of wetland pollen at different ages within the same wetland varies; for example, in wetland 161, the 1000 year old horizon is dominated by *C. asiatica* and *S. virginicus*, the 2000 year old horizon is dominated by *C. asiatica*, *S. virginicus*, *M. viminea*, *M. rhaphiophylla* and *M. teretifolia*, the 3000 year old horizon is dominated by *C. asiatica*, *S. virginicus* and *B. articulata*, and the 4000 year old
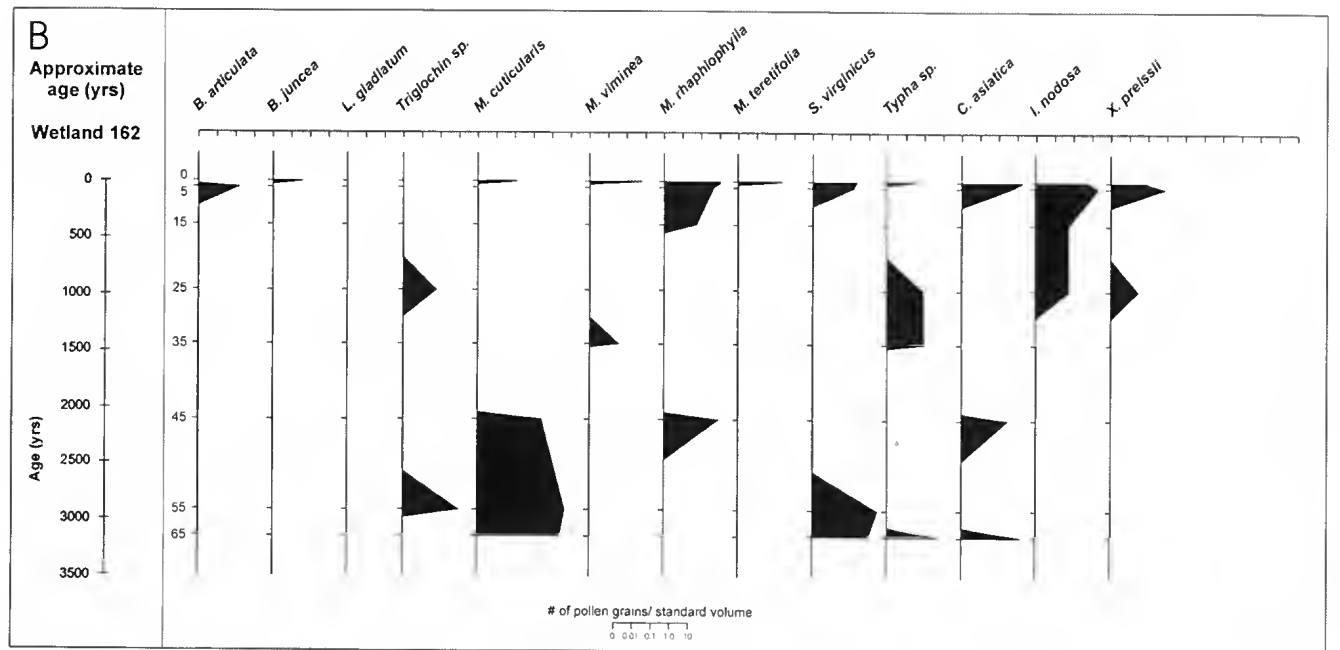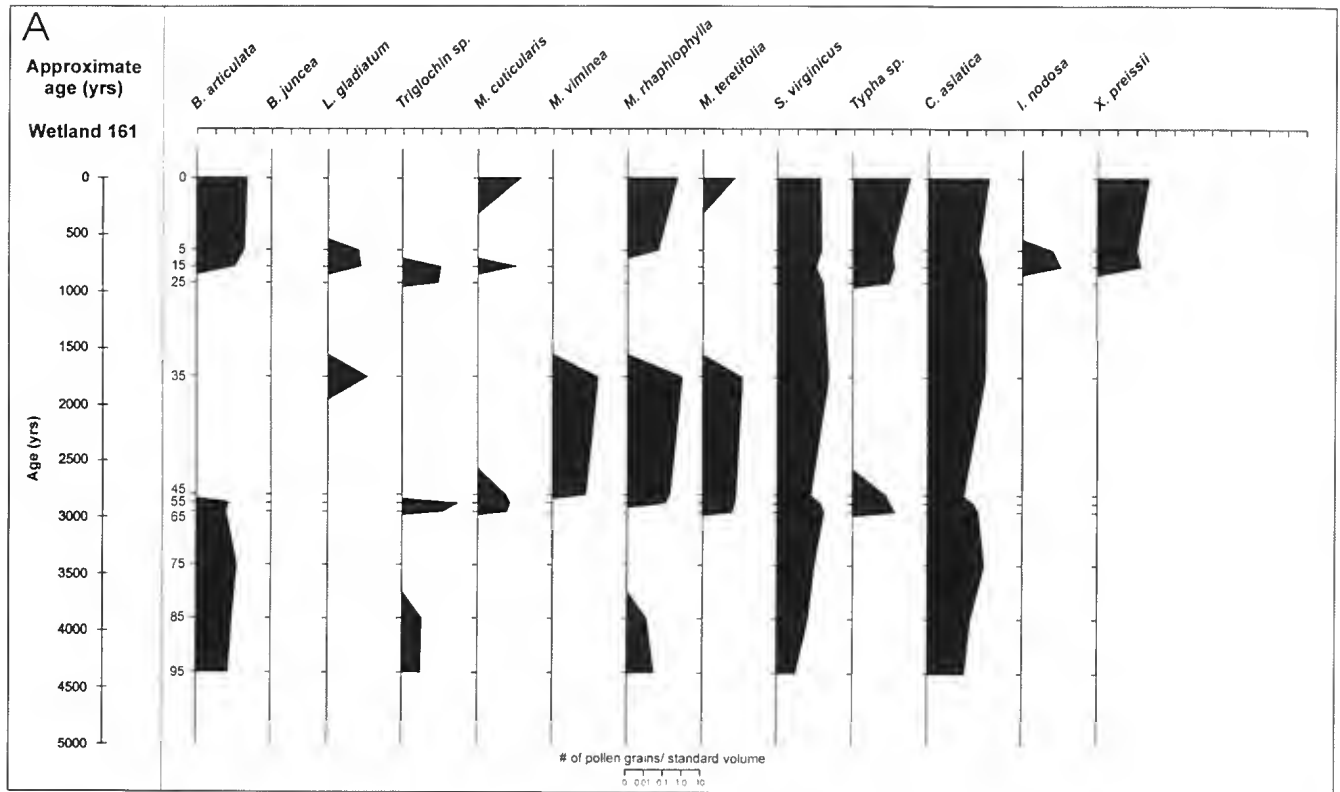
Figure 6. Graphs showing the composition of the various species of wetland pollen down the stratigraphic profile for each of the wetlands 161, 162, 163, 135, and 9–14, with the data on a chronometrically adjusted scale. The scale for pollen numbers is logarithmic.

Figure 6 (cont.)

Figure 7. Graphs showing the composition of the most abundant species of wetland pollen and upland pollen down the stratigraphic profile for each of the wetlands 161, 162, 163, 135, and 9–14, with the data on a chronometrically adjusted scale. The scale for pollen numbers is logarithmic, with only pollen abundance > 10³ noted on the graph.
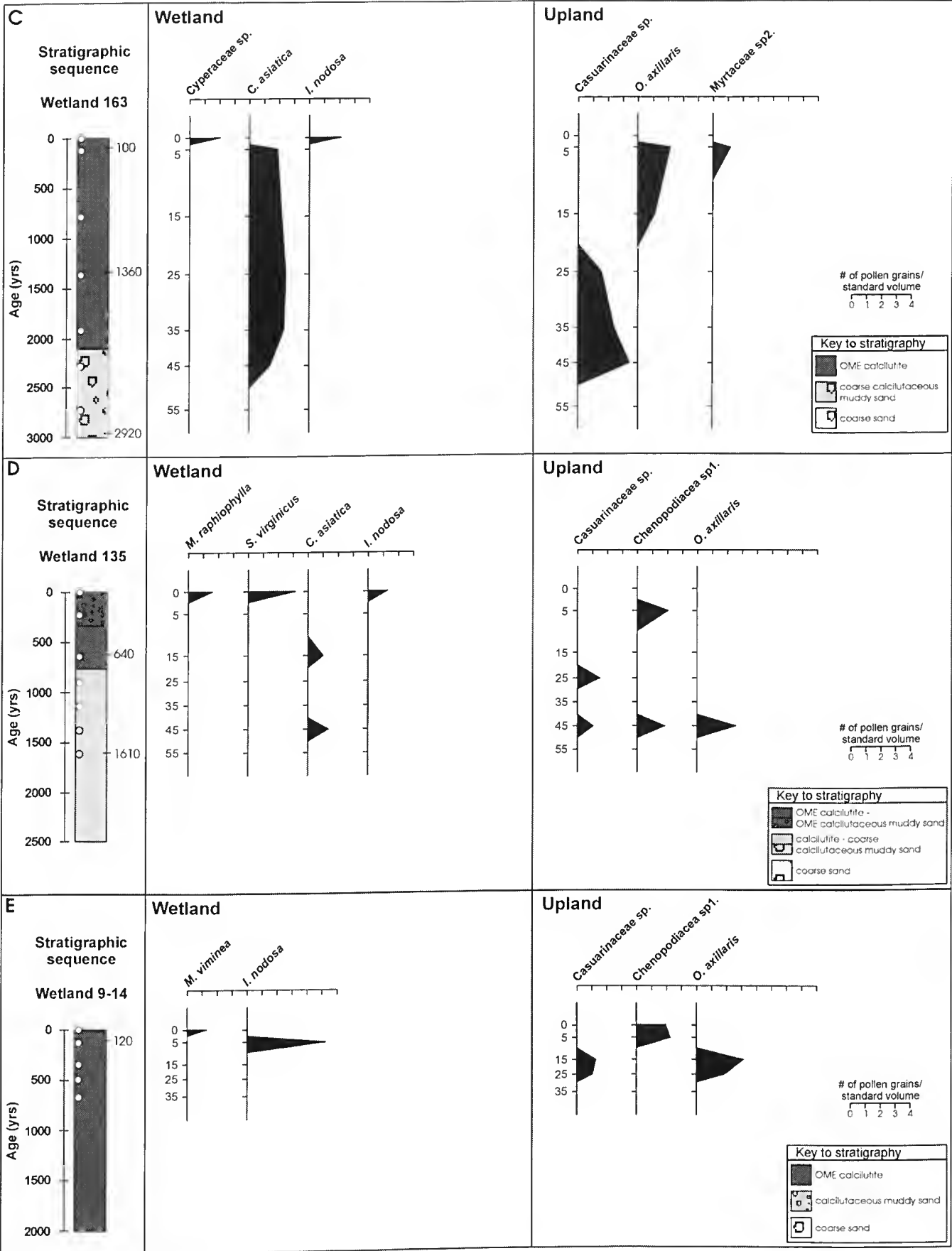
Figure 7 (cont.)

horizon is dominated by *C. asiatica*, *S. virginicus*, *M. rhaphiophylla* and *B. articulata*;

- there is an association of pollen species with sediment types;

- there are increases and decreases of marginal pollen in the down profile composition (*e.g.*, *S. virginicus*, *I. nodosa*, *L. gladiatum*, and *M. viminea* in wetlands 161, 162, 163, 135 and 9–14 in Fig. 5);

- the appearance of *I. nodosa* and *X. preissii* (*i.e.*, within the last *circa* 1500 years) is recent; and

- in subsequent development, the presence and absence of species becomes more variable in the wetlands.

The patterns of pollen derived from wetland vegetation in individual wetlands, listed above, suggest that the ancestral distribution and abundance of plant assemblages in the Becher wetlands was, and continues to be, a function of intra-basin environmental changes caused by wetland evolution (C A Semeniuk 2006). *Centella asiatica* provides specific evidence for this conclusion: firstly, there is waxing and waning of its pollen throughout the profiles; secondly, although it occurs in the early stages of wetland development in all five wetlands, it is associated with different species.

Intra-wetland changes are likely to include responses to alternating periods of above and below average rainfall resulting in the expansion and contraction of assemblages and invasion of wetland marginal species observed during this study. The evidence from the fluctuations in the pollen of marginal plant species is that wetter and drier cycles occur much more frequently than is suggested by the other categories of pollen. These fluctuations are related to real presence and absence of a particular species in the wetland basin itself as it migrates between the wetland centre and the margin in response to water availability. The regularity of these pollen peaks suggests that there is a cyclicity in the amount of rainfall which recharges the wetlands.

Accompanying these wetter and drier cycles would be changes in wind patterns (wind strength and directions), which could account for fluctuations in abundance of imported wetland pollen species within a given wetland basin. The patterns of wetland pollen abundance down profile within an isochron framework, in combination with the patterns of abundance of upland pollen as a surrogate of wind contribution, show the variable nature of the pollen record from wetland to wetland as well as the variable contribution of upland pollen by wind even in adjacent wetlands. The results underscore the complexity of the pollen record.

Examining the range of pollen species from wetland plants occurring in sediments of similar age shows that species may or may not be present in the various wetland basins at the same time, and that in most cases the abundance varies even when the composition is similar. Given that the wetland plant species pool has been consistent over the last 4500 years, differentiation between one or two plants and an assemblage is important. Plants growing in association can be interpreted with respect to hydrological and hydrochemical changes based on the environmental attributes of their current habitats (C A Semeniuk 2006). For instance, an assemblage of *B. articulata* and

C. asiatica indicates seasonal shallow inundation and fresh water, and an assemblage of *M. rhaphiophylla* and *C. asiatica*, or *M. teretifolia* or *M. viminea*, indicates seasonal waterlogging and hyposaline conditions, and possibly an expansion of species inhabiting the marginal zone, and the occurrence of *C. asiatica* and *S. virginicus* together indicates short term changes between seasonal waterlogging and dry periods. The occurrences of a single pollen type (*e.g.*, *M. cuticularis*, *C. asiatica*, and *I. nodosa*) suggest dominance within the wetland rather than pure stands. Environmental conditions associated with the occurrences of these species are as follows: *M. cuticularis* indicates either less frequent waterlogging or more saline conditions, while *C. asiatica* and *I. nodosa* indicate freshwater, seasonal wetness, and an expansion of marginal wetland species in a basin.

In contrast to pollen from wetland taxa, that derived from upland vegetation exhibits continuity down profile, but with fluctuations in abundance. This suggests that delivery of upland pollen largely has been consistent, and being exogenic it has not reflected (hydrochemical, edaphic or hydroperiod) environmental conditions within the wetlands (that of course would influence wetland vegetation composition). However, the fluctuations in abundance of upland species cannot be correlated between the separate wetland basins. Peaks in pollen numbers can be consistently related to pollen from the same families or species, and in the case of three pollen types, to specific wind directions. This heterogeneity at given isochrons from wetland to wetland corroborates the results of Semeniuk *et al.* (2006) who showed that there was a heterogeneous distribution of exogenic pollen in the surface sediments of the Becher wetland basins.

Figure 8 presents upland pollen data down the stratigraphic profile in two formats: one as numbers of total upland pollen, and the other as the proportion of the three key species contributing to that total pollen number. While total upland pollen decreased between 2000 and 500 ^{14}C yrs BP in wetland 162, the proportion of Casuarinaceae pollen increased at that time, and while there was a peak in upland pollen in wetland 135 *circa* 1400 ^{14}C yrs BP, the proportion of Casuarinaceae pollen contributing to the total pollen count decreased at that time. In terms of interpreting the history of wind patterns that delivered the regional upland pollen to a given wetland basin, the graphs showing the proportions of contributing species are a better index of wind direction, while those illustrating total upland pollen numbers are a better index of wind intensity. *Circa* 2900 ^{14}C yrs BP, the numbers of Casuarinaceae and *E. marginata* pollen increased in wetlands 161 and 162, suggesting that this period was associated with prevailing easterly winds. High numbers of pollen from Chenopodiaceae (probably *Rhagodia baccata*, a beachridge species) in wetland 162 at the same time, could be interpreted as a change to more open conditions within the wetland basin, and increases in the pollen of wetland species (*M. cuticularis*, *S. virginicus* and *Triglochin* sp.) between 3100 and 2900 ^{14}C yrs BP suggest increases in salt tolerant plants. The sediment accumulating during this period was carbonate mud, a depositional product associated with sub-regional groundwater rise (due to coastal progradation) rather than increased rainfall. In combination, these factors
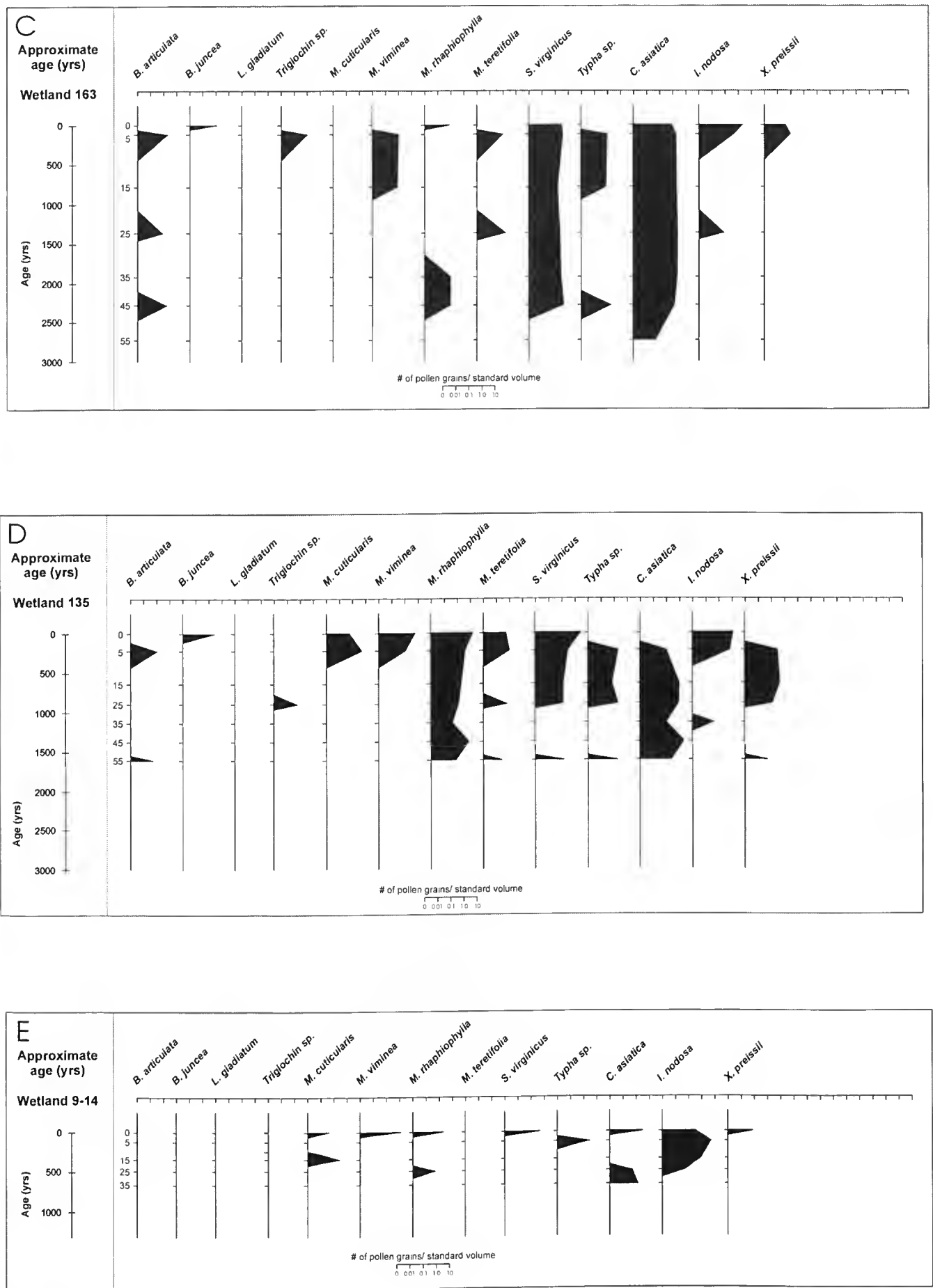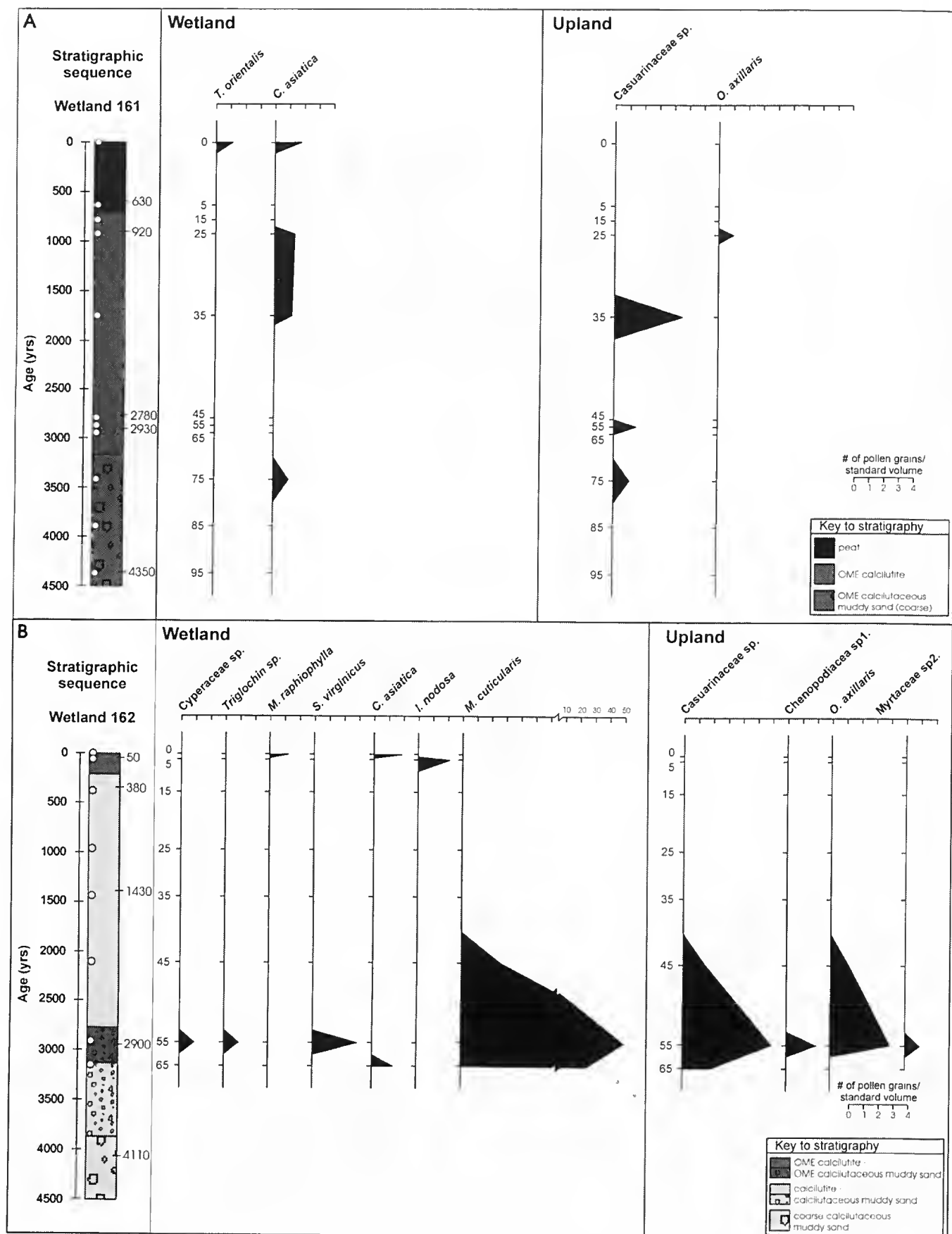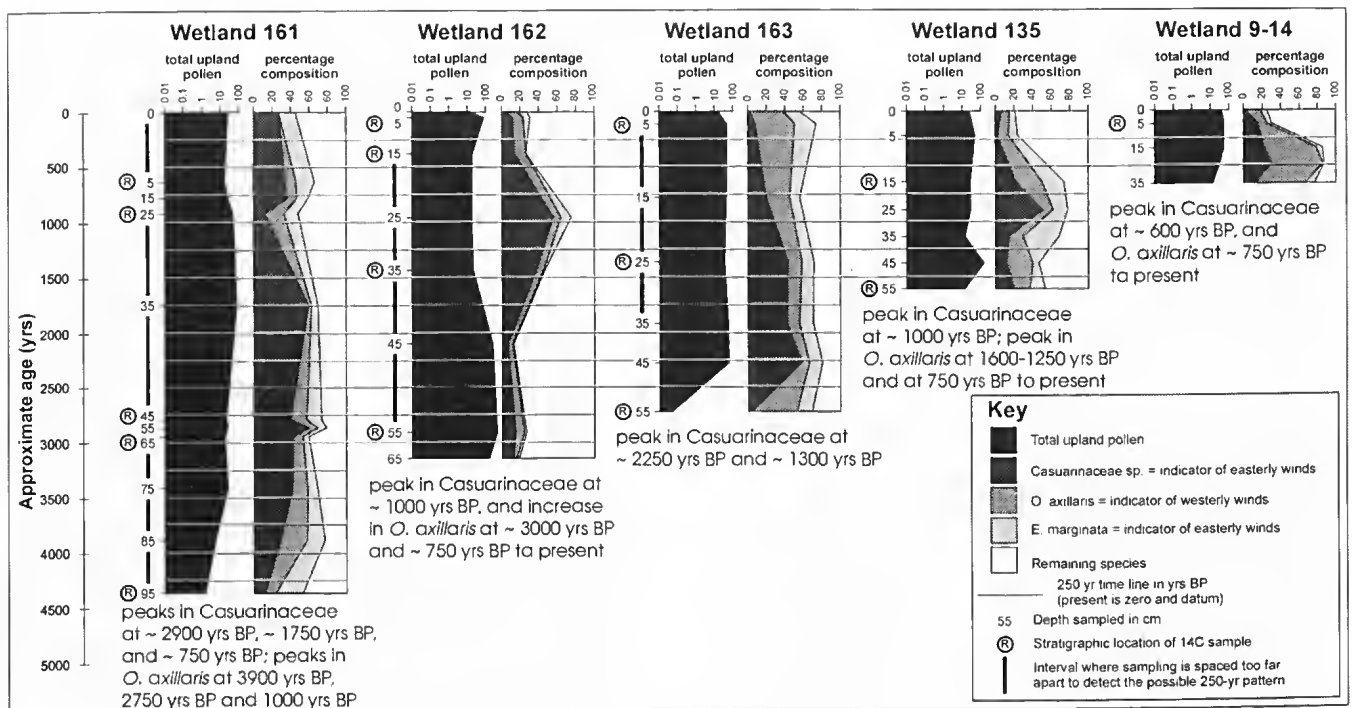
Figure 8. Graphs showing the composition of the three most abundant species of regional pollen down profile for each of the wetlands 161, 162, 163, 135, and 9–14, with the data on a chronometrically adjusted scale. The horizontal lines represent 500 year isochrons. The scale for pollen numbers is logarithmic.

suggest a wetland habitat adapting to drier climatic conditions. A similar increase in pollen from upland species in wetland 135 *circa* 1400 ^{14}C yrs BP may also indicate a period during which vegetation cover in this basin was more open, again, coinciding with carbonate mud deposition. However, supporting evidence cannot be obtained from wetlands 161 and 9–14 because there were no samples for this period, and in wetlands 162 and 163, although there are increases in the pollen of marginal wetland species (*M. viminea, I. nodosa*), and a decrease in *C. asiatica*, the composition of the wetland pollen does not suggest a sudden and intense change comparable to the arrival of *M. cuticularis* in the earlier period.

Discussion and conclusions

Whether pollen of wetland vegetation is *in situ*, derived from the wetland margins (signalling comparatively drier phases in the history of the wetlands), or transported by wind to a particular basin from other proximal or distal basins, is a critical consideration in reconstructing wetland vegetation history from the pollen record. Pollen rain and *in situ* pollen contribution, as preserved in the surface sediments of the Becher wetlands, was shown by C A Semeniuk *et al* (2006) to be heterogeneous, and the implications are that while exogenic pollen transported from distal sources preserved in the stratigraphic profile may reflect the long-term regional and sub-regional species pool, it cannot be used to reconstruct comparative vegetation history of individual wetlands. Difficulties in interpretation of the pollen record also will arise for wetland taxa when the occurrence of a given species is the result of *in situ* production *and* wind transport.

Interpreting any fossil pollen record or even its contemporary record is complex (Luly 1997), as it is influenced by the relative rates of pollen production, taphonomic considerations, vectors of transport, and in regard to aeolian transport, wind directions and wind speeds in relation to flowering times, and also whether the various flowering plant species of the vegetation assemblages are maintaining their populations sexually or asexually. A full analysis of these factors in generating a fossil or contemporary record was beyond the scope of this study.

In addition, there are other factors contributing to the difficulty in interpreting the vegetation history of each specific pollen sequence in the Becher wetlands. For instance, if the vegetation changes in its fundamental composition relatively quickly in relation to, say, 20-year and 250-year climatic fluctuations, or hydrochemical changes in local groundwater, then to detect such changes the pollen sequences within the rates of sedimentation determined by ^{14}C dating need to have been sampled on a *circa* 1 mm interval. Monitoring of vegetation over the 10 years of study by C A Semeniuk (2006) in this area indicates that many species indeed fluctuate in abundance in response to short term climatic variations. On the other hand, bioturbation, which is prevalent in the wetland sediments of the Becher Suite, locally mixes substrates over at least a 10 cm interval, obliterating any potential fine scale sequencing of pollen. This means the pollen record from the sampling interval potentially records mixed wet and dry climate assemblages that may have alternated on a 20-year or 250-year turnaround. Even the surface pollen record from the wetlands may not be reflecting the extant assemblage compositions, but rather, given the accretion rates of sedimentary material within the wetlands, and

bioturbation, a composite of up to several hundred years of record (*e.g.,* wetland 161).

Also, the relative abundance of pollen in the stratigraphic record may not reflect relative abundance of plant cover. Without autoecological and taphonomic information on the relative production rates and preservation of pollen from the various species, and the relative importance of flowering and seed production as a population maintenance strategy compared to clonal growth, the pollen record must be used with caution to interpret former relative proportions of species that contributed to the stratigraphic record. Further, without rigorous studies on the modern dispersion rates and dispersion patterns (involving identification of major wind flow paths, consistently generated eddies, and grain size fallout zones), it is not clear how far the pollen of a given species can be transported by wind and water. This means that it is difficult to determine exactly what are wholly intra-basinal contributions *versus* margin contributions *versus* possible extra-basinal contributions. The discrimination of wind transported pollen from pollen generated within the basin, in response to a medium term climate change to more arid conditions, is hampered by the fact that the species abundances and composition are likely to be the same in either situation. In addition, in the Becher wetlands, the species which are adapted to groundwater salinity are also the species that have efficient pollen dispersal mechanisms. As mentioned earlier, some of the patterns of down-profile abundances for wetland species appear to mirror patterns of abundances of upland species delivered to the wetland basin through the agency of wind (Figures 5 & 7). Yet, if increased wind activity was associated with a medium term climate change from relatively humid to more arid conditions and a concomitant increase in wetland groundwater salinity, the change in plant associations to more saline tolerant species could produce a similar pollen abundance pattern. For example, the occurrence of pollen of *Melaleuca cuticularis* and *Sporobolus virginicus* within a wetland either may signal widespread transport into a given wetland basin, or reflect the response of these species to local conditions of medium term increased groundwater salinity. This consequence is an important consideration in reconstructing the history of wetland vegetation within a particular basin.

Lastly, a major limitation to pollen studies in the Becher wetlands is the lack of finely spaced dated material. While there have been a large number of ^{14}C dates determined in the area, in terms of sedimentary sequence, and for dating the base of the sequences, there are not enough dates to be able to correlate isochronous events across the various wetland basins. For example, while there is a marked pollen event in wetland 162, with an abundance of *M. cuticularis* and *S. virginicus* at approximately ^{14}C age of 2900 yrs BP, the exact equivalent ^{14}C age interval to a precision of say, 250 years, has not been sampled in the other wetlands because of the sampling interval selected. Therefore a given pollen event in one wetland cannot and has not been correlated across to the other wetlands.

With these caveats, and awareness of the limitations described above, there are several conclusions that can be made from this pollen study about the vegetation history.

The pollen record indicates that the species pool of wetland plants colonising the Becher Suite wetlands has remained fairly stable over the last 4500 years. Both the sediments and the pollen indicate that the history of the wetlands included alternate wetter and drier periods. As these periods progressed, the species adapted to one or other of the phases came into dominance and then decreased in abundance. Overall, many of the wetland plants which are tolerant of periodic higher water salinity and changes in water periodicity continually adapted to the annual cycle of wet and dry. Over longer term climate cycles, the areas within the wetland basin under any one assemblage may contract and expand, with the prevailing hydrological and sedimentological conditions determining the composition of the vegetation. During the course of the study, the wetlands of the Becher Point region experienced a transition from relatively wet to dry to a beginning of a return to wet conditions as part of the 20-year cycle, and while there were changes in plant assemblages, the major assemblages, floristically and structurally, remained essentially the same. For example, wetland 161 remained dominated by *B. articulata,* wetland 162 remained dominated by *M. teretifolia* closed scrub, wetland 163 remained dominated by *J. kraussii,* and wetland 135 remained dominated by low forest of *M. rhaphiophylla.* The 20-year climatic patterns may not effect enough change in vegetation to be detected in the pollen record.

Wetland plants are more likely to respond to intra-wetland environmental changes than regional changes, given that the factors which determine their distribution are small scale such as geohydrology, sediment chemistry and hydrochemistry (C A Semeniuk 2006), and that the species pool of wetland plants in the Becher Point area occurs throughout the entire southwest region of Western Australia, spanning humid to semi-arid climatic zones. Other studies corroborate the findings herein that changes in wetland vegetation, particularly in seasonally inundated or waterlogged wetlands, are related to the localised fluctuations in the hydrological regime (Boyd 1990; Jenkins & Kershaw 1997). The exception to this general pattern has been the comparatively recent arrival of *X. preissii* and *I. nodosa* indicated by the occurrence of their pollen *circa* 1500 ^{14}C yrs BP. As the pollen is first recorded in each of the wetland cores around this time, and one or other of the species continues to occur in the record up to the present, it suggests a response to progressively wetter climate.

Occurrences of upland pollen taxa, in the stratigraphic (geohistorical) record, whether from regional or local ridge sources, are also variable from basin to basin. Peaks in upland pollen abundance sometimes coincide, as in wetland 162 and 135, but often do not, even when the pollen is being transported from the same source and in the same direction, *e.g., E marginata* and Casuarinaceae pollen in wetland 163 (Fig. 8). The most reliable isochronous interface in the Becher wetlands in fact is the modern surface, but here the distribution of three diagnostic upland pollen species subregionally is heterogeneous, leading C A Semeniuk *et al.* (2006) to conclude that there is no definitive pattern of distribution in upland pollen with respect to the present climatic conditions.

Use of upland pollen as a direct indicator of wind

activity in a correlative manner also has several problems. While it is clear that such pollen, where abundant, would have to be delivered to a wetland basin by wind, detailed examination of the composition of upland pollen shows variability, with different species contributing at different geohistorical times. For instance, at various times, for a given wetland basin, there is contribution from species that are located to the east of the wetlands, reflecting easterly wind dominated delivery, and there is contribution of species that are located nearer the coast, reflecting westerly wind delivery. While there may be differential spatial deposition of upland pollen in response to different wind fields and topography, it cannot even be assumed that the temporal variable deposition of the pollen within the *same* basin will reflect changes in wind patterns and hence some climate control. Further, wind patterns can be complex, and can vary in direction and strength from year to year, even within a regionally consistent climate, such that differential delivery of regional pollen taxa over time, in terms of composition and abundance, may not be signalling climate changes but rather the complexities of the aeolian processes. Also, any medium term climate changes that involved modest shifts in wind direction and speeds, as governed by oceanic and/or interior arid hinterland effects, may not have been ubiquitous across the region or sub-region. Local topography of higher than normal beachridges, or of continuous swales acting like funnels, may have influenced local deposition. Prominent marginal vegetation may have acted as interceptors to transported pollen in contrast to open basins with no barriers. In regard to dispersal of pollen of wetland species, the occurrences of upland pollen species within the wetland were used as coarse indicators of local wind and its possible contribution as a vector to deliver pollen of wetland species to a given wetland, *i.e.*, the wind that delivered upland pollen to a given wetland may also have delivered pollen from wetland species elsewhere.

Any palaeo-climatic reconstruction based on pollen from upland vegetation is further complicated by the fact that the species pool encountered on the ridges of the Becher Cuspate Foreland is similar to coastal ridge and dune vegetation between Augusta and Jurien Bay, an area which encompasses humid to semi-arid climates (Gentilli 1972), even a major climate change from humid to semi-arid, *i.e.*, a change in rainfall from 900 to < 500 mm per annum, may not be deduced from palynological investigations from coastal regions and coastal flora. A similar problem has been encountered by several palynologists (Boyd 1990; Newsome & Pickett 1993). In a study of Myrtaceae pollen in southwestern Australia, Newsome & Pickett (1993) noted that the region is dominated by sclerophyll plant communities, whose high floristic diversity is related to edaphic rather than climatic variability, and that *Eucalyptus* is widespread both as dominant and sub-dominant species within the forests and woodlands of different climatic zones.

The most reliable information on climate variability from the pollen record is provided by the marginal vegetation, firstly, because the pollen is derived from *in situ* basin vegetation, and secondly, because vegetation at the wetland margin is the most responsive to changes in water availability, increasing in cover abundance in

response to drier conditions and retreating under wetter conditions. In the Becher Point area, the pollen record of marginal vegetation shows that more regular and more closely spaced changes in rainfall have occurred than have been postulated in previous Western Australian studies.

The record of pollen in the Becher Point area only spans the past 4500 years, and so does not encompass the climate patterns over the whole of the Holocene. The changes in species abundances are commensurate with the long term change in climate from relatively dry to wetter conditions, but definitive indicators of climatic change are confounded by short and medium term changes in pollen composition and abundance. The palaeo plant assemblages, reconstructed on the analyses of pollen from wetlands and ridges of the Becher Cuspate Foreland, suggest both intra-basinal responses and climatic factors are the driving mechanisms for short and medium term vegetation changes. However, these responses, such as areal contraction and expansion, and changing dominance within an assemblage which also typify annual and short term inter-annual rainfall fluctuations, are highly individualistic.

To date, in Western Australia, there have been no published studies directed towards determining the heterogeneity of the pollen record in the large isolated wetland basins, even though studies elsewhere have indicated the complexities inherent in the accumulation of pollen (Dodson 1983; D'Costa & Kershaw 1997; Luly 1997). Equally, while there have been palynological analyses of single cores in basin wetlands in Western Australia, spanning localities from Boggy Lake (near Walpole), and Perth, to Rottnest Island (Churchill 1968; Backhouse 1993; Newsome & Picket 1993), there has not been an exploration of how representative the pollen records of these basins are of the region or subregion. C A Semeniuk *et al*. (2006) concluded that there is difficulty in interpreting regional climate patterns from the pollen record using surface pollen, because of heterogeneous and complex delivery of exogenic pollen, and in short term (temporal) variation in plant assemblages, respectively. Such heterogeneity and complexity is to be expected in the stratigraphic record. For example, using exogenic, distally derived upland pollen species, the stratigraphic variation in abundance of *Eucalyptus* and *Casuarina* in time and in different basins indicates that the isochronous influx was heterogeneous, confirming conclusions of C A Semeniuk *et al* 2006. Further, isolated single cores can lead to misleading interpretations in relation to climate changes. For example, the marked fluctuations of some key wetland species such as *Melaleuca cuticularis*, if viewed only from a single core, would imply climate changes, but multiple cores in the areas contradict this. *Melaleuca cuticularis*, rather increases and decreases in abundance as the wetland basin hydrochemically and hydrologically evolves or fluctuates. Essentially, while there are distinct small basins in Becher Point area, each wetland has had a different vegetation history. In larger basins, in areas elsewhere from Becher Point, variable vegetation (pollen) history would be manifest across concentriform, maculiform, gradiform and heteroform wetland assemblages (C A Semeniuk *et al*. 1990), particularly if they were dynamic, or in heterogeneous and dynamic

vegetated wetland margins particularly with bacataform organisation. The results from such settings would be a wetland basin filling with sediment with a heterogeneous influx of locally derived pollen types (Luly 1997), and not necessarily reflecting climate history. In this context, C A Semeniuk (2006) concluded that single basin palynological history in the Becher Point area, with lithologic changes, more likely reflects intra-basin evolution (*i.e.*, stratigraphic evolution to develop hydrochemical; evolution, and then serial vegetation responses), than regional climate history.

On the other hand, there is some evidence for climate changes in the Becher Point stratigraphic record, palynologically (as noted above) and sedimentologically. The appearance of *Isolepis nodosa* and *Xanthorrhoea preissii* at *circa* 1500 ^{14}C years BP occurs in all the wetland basins studied, and would imply that their incursion into wetland margins on the beachridge plain (regardless of the individual vegetation history of a wetland basin to that point) was broadly synchronous in the Becher Point region, implicating a climate change. The corroborative sedimentary evidence for such a climate change is the subject of another study.

In summary, in relation to climate, a combination of palynological and stratigraphic data, essentially independently corroborative information, within the *same* basin, indicating the same direction of change in environmental factors, may be used to pinpoint changes in climatic conditions. In the Becher area, examples of such changes occurred approximately 3000–2900 and 1500 ^{14}C yrs BP.

With the abundance of radiometric dates in this study area, C A Semeniuk (2006) showed that the sedimentation rates in the various wetland basins were variable. As a result, when the stratigraphic profiles are adjusted to broadly represent equal-age increments, there is internal distortion of the thickness of the sediments between any two 1000-year isochrons. This would mirror variable rates of sedimentation. The implications, however, are that to rigorously construct a climate history from cores, there needs to be enough radiometric dating to circumvent the variable sedimentation rates which would in turn affect the relative abundance of pollen, *i.e.*, the pollen record needs to be assessed within a context of rapidly accumulating *versus* condensed sequences.

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Limnadiid Clam Shrimp Distribution in Australia (Crustacea: Branchiopoda: Spinicaudata)

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Abstract

Clam shrimp (Crustacea: Branchiopoda: Spinicaudata) are ancient freshwater crustaceans inhabiting all continents of our planet. Few detailed distributional studies have been done on clam shrimp in Australia, and the few studies that have been done are quite old. Herein we report data from a series of collections across western, southern and central Australia aimed at delineating the species distributions of clam shrimp in the family Limnadiidae. We found six limnadiid species as well as several unidentified limnadiids distributed throughout Australia. The most successful sampling locations were rock pools located on granite outcrops. Three genera were collected (*Eulimnadia, Limnadia,* and *Limnadopsis*), with the former being highly female-biased and the latter two having nearly equal male/female ratios. Males were larger than females in *Limnadia* and *Limnadopsis,* and overall size differed among the three genera, with *Limnadopsis* being the largest and *Eulimnadia* being the smallest. Pool-to-pool variation was significant for both sex ratios and size, even though in many locations the pools were separated by no more than 20m. Overall, clam shrimp were found to be locally abundant, and we encourage taxonomic research to help studies such as these to correctly identify the range of species that inhabit Australia.

Keywords: *Limnadopsis, Limnadia, Eulimnadia,* sex ratios, adult size variation

Introduction

Branchiopod crustaceans are arguably the most primitive class of the sub-phylum Crustacea (Martin & Davis 2001). Branchiopods are subdivided into three orders: Anostraca, Notostraca, and Diplostraca (Martin & Davis 2001). The latter order is a combination of what was previously recognized as the 'Conchostraca' (common name "clam shrimp") and the Cladocera, both of which are now considered suborders (Martin & Davis 2001). The clam shrimp have had a tumultuous taxonomic history, and are now split into three suborders: Laevicaudata, Spinicaudata, and Cyclestherida both on the basis of their dramatic differences in morphology, (Fryer 1987; Olesen 1998) as well as on DNA comparisons (Spears & Abele 2000; Braband *et al.* 2002).

The largest of the clam shrimp suborders, the Spinicaudata, comprises of three families: Leptestheriidae, Cyzicidae, and Limnadiidae (Martin & Davis 2001). By far the largest family is the Limnadiidae, which comprises six genera: *Imnadia, Metalimnadia, Eulimnadia, Limnadia, Limnadopsis,* and *Limnadopsium* (Straskraba 1964). Only the latter four genera have been reported from Australia (Sars 1895; Sayce 1903; Dakin 1914; Webb & Bell 1979), and of these, the last two genera have been collected on no other continent, except as fossils (Tasch 1987).

Most of the reports of Australian clam shrimp have been primarily species descriptions with some location information, and most are quite old (King 1853; Sars 1895, 1896; Spencer & Hall 1896; Sayce 1903; Dakin 1914; Gurney 1927). Herein we present recently collected information about current distributions of six species of Spinicaudata in the family Limnadiidae, including information on sex ratios and size characteristics.

Methods and Materials

We used a combination of field collections and soil hydrations in the laboratory to determine species composition and sex ratios for the 23 locations we sampled (Table 1; Fig. 1). Our field collections included two large collection trips. The first was centred in south-west Western Australia (March 4 to April 27, 2003) while the second was a seven-week trip through central Australia, starting in South Australia, travelling up into the Northern Territory, and finishing in Western Australia (April 5 to May 19, 2004). All collecting trips included a combination of live collections (when shrimp were available) and soil collections for later hydrations in the laboratory. Live shrimp were preserved in 95% ethanol and transported back to the laboratory for species identification, size measurements, and sex ratio calculations.

Soil hydrations consisted of taking a small sample of field-collected soil (50–250 ml soil), placing the soil in the bottom of a glass aquarium (2–35 litres), and adding deionized water. The aquaria had small air stones for continuous aeration. Two laboratory locations were used: one at the University of Western Australia and the other at the University of Akron. For the former, aquaria were

placed on a covered balcony, thus affording them natural light and temperature conditions (late summer, 2003). For the latter, aquaria were placed in a temperature controlled wet lab, and kept under continuous artificial light (Durotest Sunlight Simulating fluorescent bulbs) and constant temperatures (26–28°C). Food was a combination of 1:1 ratios of baker's yeast and ground flake food for algae-eating fish, which was suspended in water (1 gm food mix per 100 ml water) and supplied to the aquaria *ad lib* once per day. Such laboratory conditions have demonstrated optimal growth and survival for other Limnadiid shrimp (Weeks *et al.* 1997).

Statistical analyses were performed using JMP (SAS Institute 2003). Differences in sex ratios among pools within locations were assessed using contingency table analyses and differences in size among species, between sexes, and among locations within species were assayed using ANOVA tests.

Results

Limnadiid clam shrimp were collected live or reared from soil from 24 separate sites (Table 1; Fig. 1). Because no comprehensive key for Australian clam shrimp is available, and due to the poor species descriptions from primarily older publications, species identifications were quite difficult. Therefore, from these 24 sites, six Limnadiid species were identified: two *Eulimnadia* (*E.*

feriensis Dakin, 1914 and *E. dahli* Sars, 1896), three *Limnadia* (*L. badia* Wolf, 1911, *L. sordida* King, 1855, and *L. stanleyana* King, 1855), and one *Limnadopsis* (*L. tatei* Spencer & Hall, 1896). Of these six species, *E. feriensis* and *E. dahli* were the most widespread, being collected from 7 and 5 separate locations, respectively. *Limnadia badia* was found in three locations, all geographically close to one another (two rock pools and an earthen pool). *Limnadia sordida* was found in two locations (one earthen pool and one rock pool) as was *Limnadopsis tatei* (both earthen pools). *Limnadia stanleyana* was collected from only a single location.

We were unable to determine species from an additional six locations; one sample was classified as *Limnadia* and five were classified as *Limnadopsis* (Table 1). The shrimp in these locations differed in small ways from the other, named species, but were different enough to cause us to question their true identifications. Thus we lumped these unknowns into the "spp." category by genera.

Sex ratios varied dramatically among species and locations, ranging from 69% males to 100% females. However, sex ratios were rather consistent within genera, with the *Eulimnadia* populations being heavily female-biased and the *Limnadia* and *Limnadopsis* populations having a consistent 1:1 sex ratio (Table 1). Among the *Eulimnadia* locations, there were four locations with exceptionally low male proportion (<2%), while the
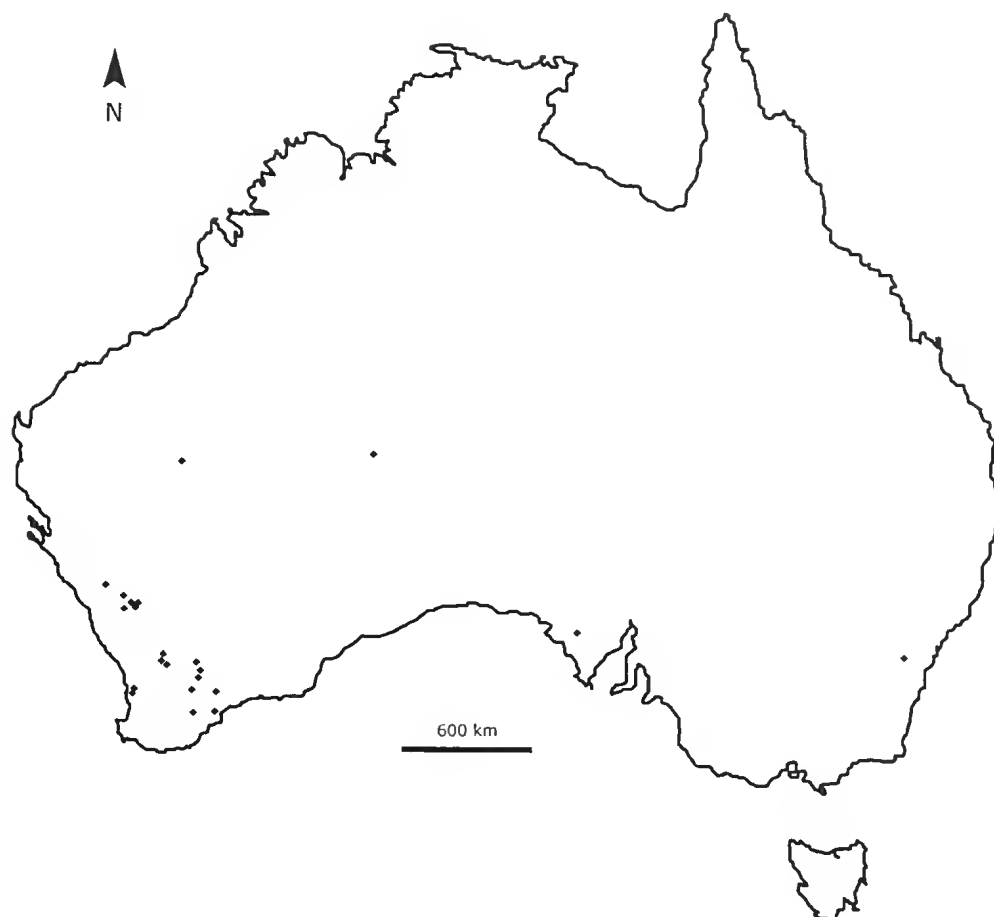
Figure 1. Sampling locations.

Table 1

Location information and sex ratios for the collected limnadiid clam shrimp.

Species	Location	Latitude	Longitude		Total			(L)ab or
					Males	Females[a]	%Male	(F)ield
Eulimnadia feriensis	Cairns Rock	S31° 51.517'	E118° 50.650'		44	238	15.6%	L
	Outcrop	S31° 51.414'	E117° 36.894'		0	128	0.0%	L
	Tammin Rock	S31° 40.195'	E117° 30.806'		2	182	1.1%	F & L
	Wanara Claypan	S29° 32.750'	E116° 43.866'		3	19	13.6%	F
	Wanara Rock	S29° 31.450'	E116° 47.533'		8	34	19.0%	F & L
	Wave Rock	S32° 26.538'	E118° 53.908'		9	63	12.5%	L
	Yorkrakine Rock	S31° 25.405'	E117° 30.835'		28	167	14.4%	L
				Overall	44	831	10.2%	
Eulimnadia dahli	Pygery Rocks	S32° 59.165'	E135° 28.238'		0	4	0.0%	F
	Bunjil Rocks	S29° 37.833'	E116° 23.633'		27	81	25.0%	L
	Green Rock	S29° 31.250'	E116° 38.340'		44	98	31.0%	F
	The Humps	S32° 18.885'	E118° 57.574'		17	52	24.6%	L
	Kadjii-Kadji	S29° 8.233'	E116° 24.833'		0	4	0.0%	L
				Overall	88	239	26.9%	
				Overall *Eulimnadia*	182	1070	14.5%	
Limnadia badia	Wanara Rock	S29° 31.450'	E116° 47.533		14	9	60.9%	F
	Dunn Rock	S33° 20.110'	E119° 29.370'		18	32	36.0%	L
	Dingo Rock	S33° 0.567'	E118° 36.133'		6	6	50.0%	L
				Overall	38	47	44.7%	
Limnadia sordida	Armadale Road	S32° 8.560'	E115° 57.200'		13	12	52.0%	F & L
	Wanara Claypan	S29° 32.750'	E116° 43.867		11	5	68.8%	F
				Overall	24	17	58.5%	
Limnadia stanleyana	Kanangra Walls	S33° 59.933'	E150° 5.133'		140	132	51.5%	F & L
Limnadia spp.	Albany Hwy Rail	S32° 5.280'	E116° 0.370'		5	4	55.6%	L
				Overall *Limnadia*	207	200	50.9%	
Limnadopsis tatei	Kadji-Kadji	S29° 8.233'	E116° 24.833'		63	58	52.1%	L
	Lasseter Hwy.	S25°13.330'	E132° 02.544'		14	14	50.0%	F
					77	72	51.7%	
Limnadopsis spp	Melaleuca Swamp	S33° 53.917'	E118° 31.833'		1	6	14.3%	L
	Pabellup Swamp	S34° 7.050'	E119° 26.833'		14	24	36.8%	L
	Pilbarra, W.A.	S 24° 7.550'	E 119° 41.600'		3	3	50.0%	L
	Tjulun RH, WA	S25° 24.717'	E127° 35.183'		2	4	33.3%	F
	Tardun CBC Dam	S28° 43.033'	E115° 49.067'		9	7	56.3%	L
				Overall *Limnadopsis*	106	116	47.7%	

[a]*Eulimnadia* "females" are most likely hermaphrodites, as in all other *Eulimnadia* species so far examined (Weeks et al., 2006).

remainder had 13–31% males. The average sex ratio among all *Eulimnadia* locations was 14.5% males (Table 1).

The sex ratios were much closer to 1:1 in the remaining two genera. *Limnadia*'s overall sex ratio was 50.9% male (Table 1), with *L. badia* showing a slight female bias (55% females), *L. sordida* a slight male bias (59% males) and *L. stanleyana* much closer to 1:1 (51.5% males). *Limnadopsis'* overall sex ratio was 47.7% male, with *L. tatei* having 51.7% male (Table 1).

Collections were made at more than one pool for five separate locations: three for *E. feriensis*, one for *E. dahli*, and one for *L. stanleyana* (Table 2). In the two *Eulimnadia* species, sex ratios ranged quite dramatically: in the three *E. feriensis* locations (12 pools total), sex ratios ranged from 0.0 to 100% males, with an average of 9.0% males while in the single *E. dahli* location (6 pools total) sex ratios ranged from 0.0 to 50% males, with an

average of 31.0% males. In the three *L. stanleyana* pools (Kanangra Walls), sex ratios had lower variation, ranging from 22 – 56% males with an average of 51.5% males. At each *Eulimnadia* location, at least one pool had no males collected or reared from soil. In fact, a series of contingency table analyses revealed significant pool-to-pool variation in sex ratios among pools in all but the Tammin Rock location, even though the pools within locations were separated by no more than 20 meters.

Collections of 328 total shrimp from six species (*Eulimnadia feriensis, Eulimnadia dahli, Limnadia badia, Limnadia stanleyana, Limnadia sordida,* and *Limnadopsis tatei*) were made from nine separate pools to compare sizes within and among species. Of these six species, *E. feriensis, E. dahli,* and *L. sordida* were the smallest followed by *L. badia, L. stanleyana,* with *Limnadopsis* the largest of the six (Fig. 2). These differences were significant ($F_{5,316} = 1744$; $P < 0.0001$).
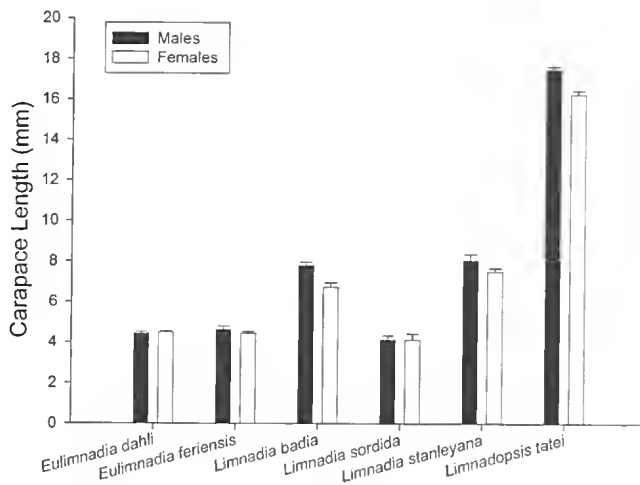
Figure 2. Relative male and hermaphrodite size (measured as carapace length) for *Eulimnadia dahli, Eulimnadia feriensis, Limnadia badia, Limnadia sordida, Limnadia stanleyana,* and *Limnadopsis tatei* (Lasseter Hwy.). Error bars portray one standard error of the mean.
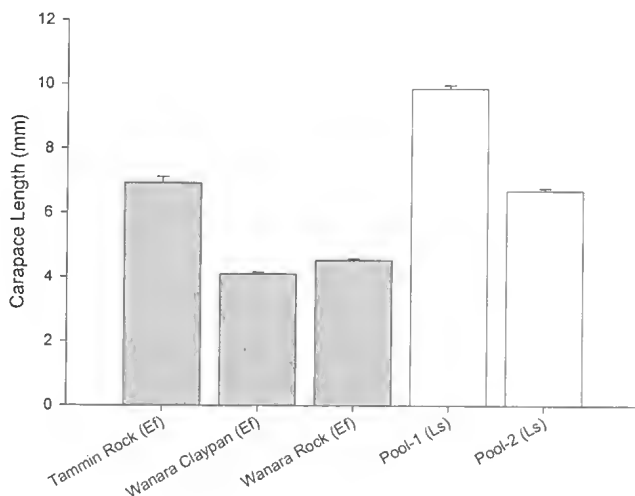
Figure 3. Size (carapace length) variability among pools for *Eulimnadia feriensis* (Ef – gray bars) and *Limnadia stanleyana* (Ls – white bars). Error bars portray one standard error of the mean.

Males were larger than females, on average ($F_{1,316}$ = 22.3; P < 0.0001), but this difference depended on species, with the size difference being more dramatic with the larger species ($F_{5,316}$ = 6.3; P < 0.0001; Fig. 2). Size also significantly varied among locations within species (Fig. 3). Within *E. feriensis*, the Tammin Rock location had the largest shrimp ($F_{2,82}$ = 72.9; P < 0.0001; Fig. 2), while for Kanagra Walls collections, the *L. stanleyana* collected from Pool-1 were significantly larger than those from Pool-2 ($F_{1,32}$ = 504.7; P < 0.0001; Fig. 3).

Discussion

The distribution and ecology of clam shrimp is under-studied worldwide, and Australia is no exception. Even though some work has been carried out on Australian clam shrimp in the past 20 years (Timms 1986; Timms & Richter 2002; Richter & Timms 2005), most studies of

Australian clam shrimp are over 35 years old (Wolf 1911; Dakin 1914; Glauert 1924; Henry 1924; Bishop 1967, 1968, 1969), and many species have not been reported in the literature for over a century (King 1853; Sars 1895, 1896; Sayce 1903). One might assume that this neglect is due to a difficulty in locating these "elusive" crustaceans, but our collecting trips proved this to be incorrect: clam shrimp are locally abundant in several areas of Australia.

The pools in which we were most successful at collecting limnadiid clam shrimp were rock pools located in Western Australia. We had 100% success in collecting either live clam shrimp or rearing shrimp from soil collected from rocky outcrops that had at least one pool of 10 cm or more in depth. Twelve of the 24 collection locations were on granite outcrops (Bunjil Rocks, Cairns Rock, Green Rock, Outcrop, Tammin Rock, The Humps, Wanara Rock, Wave Rock, Yorkrakine Rock, Pygery Rocks – Eyre Peninsula, Dingo Rock, and Dunn Rock), with most of these sites being populated by *E. feriensis, E. dahli,* or one of the *Limnadia* species (Table 1). *Limnadopsis* was never found in rock pools, but rather preferred swamps or claypans.

Sex ratios among species were consistent with their inferred mode of reproduction. Clam shrimp in the genus *Eulimnadia* have commonly been found to be female biased (Sassaman 1995). In fact, *Eulimnadia* has been described as an "androdioecious" group (Sassaman & Weeks 1993), with males and hermaphrodites (rather than females) and with populations heavily biased towards hermaphrodites (Weeks, *et al.* 2006). Indeed, the average male proportion in populations of *E. texana* is ~23% (Weeks & Zucker 1999). Thus, the observations that the Australian *E. feriensis* populations are ~10% males and that the *E. dahli* averaged ~27% male are consistent with an androdioecious mode of reproduction for these clam shrimp (Weeks, *et al.* 2006). Further work will need to be done to confirm this inference.

The sex ratios of the *Limnadia* and *Limnadopsis* were also completely consistent with their inferred mode of reproduction. Except for one species of *Limnadia* (*L. lenticularis*), all reports of sex ratios for both genera have been either 1:1 or male-biased (Sassaman 1995). These data have been used to infer that species in both genera are obligately outcrossing sexuals (Sassaman 1995), and preliminary results from laboratory-based rearings also confirm this inference: isolated females from these genera do not move eggs to their brood chambers when males are absent, and viable eggs have only been collected from females that have been paired with males (Weeks, pers. obs.). Thus, the Australian species of *Limnadia* and *Limnadopsis* are quite likely obligately outcrossing sexual species.

The significant differences in sex ratios among pools within a location were not expected. Pools separated by no more than 20 m varied from 0 to ~50% males in both *E. feriensis* and *E. dahli*, and three of four *Eulimnadia* locations had significant variation among pools in male:female (hermaphrodite) ratios (Table 2). The differences among pools for *L. stanleyana*, although still significant, were much smaller than for *Eulimnadia*, ranging from 22–56% males. Such high among-pool variation in both species suggests either that these pools have exceptionally divergent selection pressures for male

Table 2

Sex ratios per pool at five clam shrimp locations. Juvs = juvenile shrimp.

Species	Location	Pool	(F)ield or (L)ab	Juvs	Males	Females[a]	%Male	Chi-Square	P-value
Eulimnadia feriensis[a]	Yorkrakine Rock	1	L	0	9	29	23.7%		
		2	L	0	0	36	0.0%		
		5	L	0	4	25	13.8%		
		9[b]	L	0	2	1	66.7%		
		10	L	0	13	76	14.6%	13.4	0.0039
	Tammin Rock	1[b]	F	0	2	0	100.0%		
		2	L	1	0	74	0.0%		
		9	L	0	0	108	0.0%	0.0	1.0000
	Wanara Rock	3	F	6	1	9	10.0%		
		4	F	26	7	7	50.0%		
		7[b]	F	6	0	6	0.0%		
		8	F	0	0	12	0.0%	12.2	0.0022
		Total		39	38	383	9.0%		
Eulimnadia dahli[a]	Green Rock	1	F	52	20	22	47.6%		
		2	F	34	6	6	50.0%		
		3[b]	F	12	0	7	0.0%		
		4	F	31	12	42	22.2%		
		7	F	4	0	11	0.0%		
		8	F	11	6	10	37.5%	17.3	0.0017
		Total		144	44	98	31.0%		
Limnadia stanleyana	Kanangra Walls	1	F	12	3	8	27.3%		
		2	F	16	5	18	21.7%		
		3	L	0	132	106	55.5%	12.8	0.0017
		Total		28	140	132	51.5%		

[a]*Eulimnadia* "females" are most likely hermaphrodites, as in all other *Eulimnadia* species so far examined (Weeks et al., 2006).
[b]Pool not considered for the contingency table analysis due to small sample size.

proportions, or that migration and gene flow among pools is quite limited, thus allowing sex ratios to be highly influenced by colonization events and genetic drift.

Although wind is commonly considered as a major cause of branchiopod dispersal among habitats, Brendonck and Riddoch (1999) found limited evidence for such dispersal of anostracan eggs, collecting wind blown eggs at < 2% of 423 sites studied, and then only at distances no more than 50 cm from their source. These results suggest that wind dispersal is quite limited for branchiopod eggs.

Gene flow has also been estimated to be quite limited. Davies *et al.* (1997) found high among-population genetic differentiation (average F_{ST} = 0.66) in the anostracan *Branchinecta sandiegonensis*, indicating low levels of between-pool migration. Brendonck *et al.* (2000) also found high genetic differentiation (average F_{ST} = 0.29) among three pools of the anostracan *Branchipodopsis wolfi* in rock pools in Africa. In the clam shrimp *Eulimnadia texana*, Weeks and Duff (2002) reported F_{ST} values of 0.28 and estimated migration rates to be ~0.6 migrants per generation among pools. An analysis of a subset of these pools that were separated by no more than 100 m still revealed significant genetic sub-structure (F_{ST} = 0.16) and estimates of migration among pools of 1.3 migrants per generation. All of these studies suggest that migration rates among pools might be quite limited, and this low migration rate could explain the significant variation among pools in male proportion found in the current study.

Size also differed significantly, among species, among pools within species, and between the sexes. The among-pool differences in size are likely due to either density effects and/or to differences in age since hydration for the various pools surveyed. High density is known to cause reduced growth rate per individual in *E. texana* (Weeks & Bernhardt 2004). Because our samples were from the field, we had no control over either factor, and thus such pool-to-pool variation was likely a reflection of one or both of these factors.

The among-species and between-sexes differences are more likely to be at least partially a reflection of genetic differences. Because the between-sexes measures were taken from individuals from the same pools, it is likely that these are reflective of genetic differences between the sexes, with males growing larger than females, at least in *Limnadia* and *Limnadopsis*. Size differences between the sexes were much less evident in *E. feriensis* and *E. dahli*, which is consistent with other studies on *Eulimnadia* wherein the size range of males and females largely overlaps, but the largest males are slightly larger than the largest females (Knoll & Zucker 1995). Larger male size has been shown to confer greater outcrossing probability in clam shrimp (Knoll & Zucker 1995), and thus in species with greater levels of outcrossing (*i.e.*, *Limnadia* and *Limnadopsis*) there may be greater selection for larger males than in species which regularly self-fertilize (Sassaman 1989; Weeks & Zucker 1999).

The significant difference in size among the three limnadiid genera is also likely to be partly genetically determined. Laboratory rearings of all three genera

under common garden conditions suggest a greater ultimate size is reached by *Limnadopsis*, followed by *Limnadia* and finally by *Eulimnadia*. Larger size is correlated with a longer age to maturity and a greater lifespan of the former two genera relative to *Eulimnadia* (Weeks, pers. obs.). Thus, although the ages at collection for the three species were not known and density per pool was uncontrolled, the general size differences among genera is likely reflective of a general difference in life history characteristics of these three genera.

To summarise, limnadiid clam shrimp were found to be quite abundant and widespread in temporary pools in Western Australia. Rock pools on granite outcrops were particularly well populated with limnadiids, although no species of *Limnadopsis* were found in such pools. We should note that we only made these collections in two large collecting trips, and that our field collections therefore may under represent the true limnadiid diversity of these areas across the seasons. We hope that these results will encourage others to look for these interesting freshwater crustaceans, and we strongly recommend that the development of an Australian taxonomic key would greatly increase the reporting of these fascinating crustaceans.

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The large branchiopods (Crustacea: Branchiopoda) of gnammas (rock holes) in Australia

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Abstract

Small water-filled hollows in exposed rock masses occur across Australia and are particularly common in south-western Australia on granite. Sixteen species of large branchiopods, comprising six anostracans, eight conchostracans and two notostracans occur in these gnammas, with at least *Branchinella longirostris, Limnadia badia* and *Caenestheriella maraie* in south-western Australia and *Limnadia urukhai* in south-eastern Queensland obligate inhabitants. In Western Australia five common species (the three above plus *Lynceus maclayeanus* and *Eulimnadia dahli*) are ecologically separated by differences in seasonal occurrence, habitat and feeding requirements. The high diversity in south-western Australia is explained by its great age, rock pools acting as refugia in dry climatic periods, and separation from eastern Australia.

Key words: *Branchinella longirostris, Limnadia badia, Caenestheriella maraie, Lynceus maclayeanus,* niche separation, co-occurrences, south-western Australia.

Introduction

Rock holes, or gnammas as they are known throughout Western Australia and beyond (Bayly 1999), are common and widespread landscape features in Australia. This is particularly so on granitic rocks and in arid/semiarid regions (Carnegie 1898; Bayly 2002).They are semantically equivalent to 'weather pits,' 'solution pits,' 'granite pits,' 'rock basins,' 'pot holes,' 'pits,' and 'pans' (in context, not clay pans or playas) (Smith 1941; Twidale & Campbell 1993; Brendonck *et al.* 2000, Graham in press).

The few studies on Australian gnammas have focused on their geomorphology (Twidale & Corbin 1963; Campbell & Twidale 1995) and community ecology (Bayly 1982, 1997; Bishop 1974; Pinder *et al.* 2000), though Bishop (1967a, 1967b, 1969) considered the autoecology of the conchostracan *Limnadia stanyleyana.* Early taxonomical studies by Wolf (1911) described the anostracan *Branchinella longirostris* and the conchostracan *Limnadia badia* from granitic gnammas in south-western Australia, and more recently Webb & Bell (1979) described *Limnadia urukhai* from similar pools in south-eastern Queensland. Otherwise references to large branchiopods of Australian gnammas are little more than species lists, sometimes incompletely identified (Main 1967; Jones 1971; Pinder *et al.* 2000; Bayly 2001, Timms 2002; Timms & Geddes 2003).

The above studies point to a much richer fauna in south-western Western Australia than elsewhere in Australia. Therefore the aim of this paper is to systematically investigate the composition and biogeography of the large branchiopod fauna of gnammas in southwestern Australia, but in a context of Australia as a whole.

Methods

Fifty-two granitic outcrops throughout south-western Western Australia, bounded by Cue in the north, near Balladonia in the east, Holland Rocks in the south and near Perth in the west (Fig. 1) were visited between July and September 2003. The northern, eastern and western limits are near the edge of major outcrops of granitic rocks (Myers 1997); in the south there are many more significant outcrops south of Wagin-Pingrup, but previous studies (Bayly 1982, 1997; Pinder *et al.* 2000) have not recorded large branchiopods on them.

My previous field experience and that of Bayly (1997) suggested larger gnammas had more invertebrate species, and that pools > 10-20 cm deep when full and one to two metres diameter were large enough to contain most species. Stochastic events and different seasonal development strategies may limit the fauna actually present at anyone time. For maximum diversity, pools were visited when full or nearly so and only those deeper than 10 cm and larger than 50 cm diameter were targeted, with an emphasis, if possible, on larger pools. To simplify fieldwork and analysis, gnammas were divided into four types:

- Small shallow pan gnammas generally 0.5 to 1 m in diameter, and 10–20 cm deep when full.

- Larger, deeper pan gnammas generally 2–5 m in diameter and 20–40 cm deep when full.

- Pit gnammas which although of small diameter (50 cm to 1–2 m), were deeper than 0.25 m, often up to 1–2m deep.

- A variety of other contact pools adjacent to the base of the rock or artificially dammed on the rock. Most had significant contact with soil and were > 2 m diameter.

At each granitic outcrop up to 10 smaller pans and up

Figure 1. Map of localities sampled for large branchiopods in south-western Australia.

to 10 larger pans, if available, were sampled together with any pit gnammas and associated pools that were found on the rock (some pit gnammas are hidden by capping stones and difficult to locate). A round household sieve, 17 cm in diameter, 7 cm deep and of mesh size 1.4 mm, was moved to and fro through each pool for 1–3 minutes depending on numbers caught and any large branchiopods caught transferred to a sorting tray, and then preserved in 80 % ethanol.Species were recorded on a presence-absence basis for each pool.

I adopted a similar approach for some granitic outcrops (Mt Wudinna, Turtle Rock, Polda Rock, Pooncarra Rock, Pildappa Rock and Peella Rocks) near Wudinna and Minnipa in the Upper Eyre Peninsula, South Australia. Only a summary of this work is presented here. In the winter of 2004, I revisited some of the Western Australian sites studied in 2003 plus many others. This time only a general assessment was made of species present on each granite outcrop and the data used to fill out the species distribution maps.

Some material from other rock pools, or collected at

other times of the year from gnammas in Western Australia were made available to this study by colleagues (see Appendix 1). Other data were gleaned from the literature and from collections in the Western Australian Museum (WAM).

Results

Four species (*Branchinella longirostris, Limnadia badia, Caenestheriella mariae* and *Lynceus macleayanus*) were collected commonly from most of the 52 granite outcrops studied in Western Australia (Table 1). The first three are obligate inhabitants of gnammas and probably do not occur much beyond the distributions shown in Figures 2–4. The core area for these three species is an irregular oval area bounded by Kalgoorlie, Balladonia, Ravensthorpe, Wagin, Northam, Dallwallinu and Mt Magnet, with minor deviations for each species. *Caenestheriella mariae* is the most limited with no populations found in the southwest, *B. longirostris* also is apparently absent from the southwest and the far

Table 1

Distribution and numbers of large branchiopods in granitic rock pools in Western Australia as determined by field work in 2003.

Rock No.	Outcrops Name	Deep pans						Shallow pans				Pits		Other pools				
		No.	Bl	Lb	Cm	Lm	Tr	No.	Bl	Lm	Cm	No.	Lm	No.	Bl	Lm	Cm	Cp
1	Newmans Rks	2	1		1			10		1								
2	Disappointment Rks	10	3	7				10		4								
3	McDermid Rks	10	7	8	1			10		6								
4	Bushfire Rks	2	1	2	1			10		4								
5	King Rks	5		5	2			10		6								
6	Graham Rks	4						5										
7	Wave Rk	10	2	6				10		1								
8	Anderson Rks	10	5	7				10		4		3						
9	Frog Rk	10	2	4				10		1								
10	Jilbadgie Rk	10	4	6				10		3								
11	Strawberry Rks	1	1	1				5		4								
12	Moorine Rk	2	2	2				5		3								
13	Coarin Rk	2		2				5		2								
14	Bulgin Rk							2										
15	Yorkrakine Rk	5	3	4				10		4								
16	Yarragin Rks	5	3	3				10		3								
17	Elachbutting Rks	10	3	6	2			10		2								
18	Baladjie Rks	1	1	1	1			10	1	3								
19	Weowannie Rks	5	4	4				5		1								
20	Sanford Rks	10	3	4				5		2								
21	Corrigin Rk							10		1								
22	Boyagen Rk	2						5										
23	Sullivan Rk							2		2								
24	Petrudor Rk							10		4				2*		2		1
25	Cleary Rk							10		5				1^		1		
26	Scotsmans Road'							10		5		2	1					
27	Washington Rks							10		4		2	1					
28	Remlap old hstead'	6	2	2	1			10		2								
29	Paynes Find Rks	10	7	4	2			10		3				1*		1		
30	Wanarra Rks	10	3	1	2			10			1			1^	1	1	1	
31	Green Rk	0						10						1*		1		
32	Wardagga Rk	10	6	2	4			10	1		1			5*		1		
33	Daggar Hills	10	3	1				10										
34	Walga Rk	4	2		4		1	10										
35	Afghan Rk	0						8										
36	Barlongi Rk	0						0										
37	Trainer Rks							10						1				
38	Rainy Rks							10						2				
39	Old Rainy Rks	5	1	3				10				1	1					
40	Hospital Rks	10	4	2				10		1								
41	25 Mile Rks							10		4								
42	Buldania Rk	3		1				10		2		5	3					
43	McPherson Rk	10	2	6		1		10		1								
44	Lilian Stokes Rks	10	1	4	1	1		10		2								
45	Mt Madden	10	1	3		1		10										
46	Dingo Rk							10		7								
47	Jilakin Rk							10		1								
48	Puntapin Rk							10		2								
49	Yillaminning Rk	0						0										
50	Boulder Rk	0						2										
51	Holland Rks	10		9	1	1		10		3		2	2					
52	Xantippe Rks	6	5	6				10#										

*plunge pools
^artificial dam
#all dry when visited

No = number of pools sampled; Bl = *Branchinella longirostris*, Lb = *Limnadia badia*, Cm = *Caenestheriella mariae*(recorded as *Cyzicus* sp. by Bayly (1997) and Pinder (2000)); Cp = *Caenestheriella packardi*; Lm = *Lynceus macleayanus*, Tr = *Triops* near *australiensis*

southeast, while *Limnadia badia* penetrates further south and southeast than other species (Figures 2–4). *Lynceus macleayanus* occurs within this area (Fig. 5), and elsewhere in the state and in South Australia, but almost always in gnammas or pools adjacent to rock outcrops (M. Zofkova, pers. comm.). A fifth species, *Triops* sp. near *australiensis* occurred rarely in one pool on Walga

Rock in 2003 and 2004 (it was also there in 2001, author's unpubl.data), and also in many pools on Ballan Rock in 2004.In addition this species is known from a pan in the Pilbara (northwestern WA)(A. Pinder, pers.comm.).

Detailed analysis of occurrence data on each granite outcrop showed each of the common species had different habitat preferences (Table 1). *Branchinella*
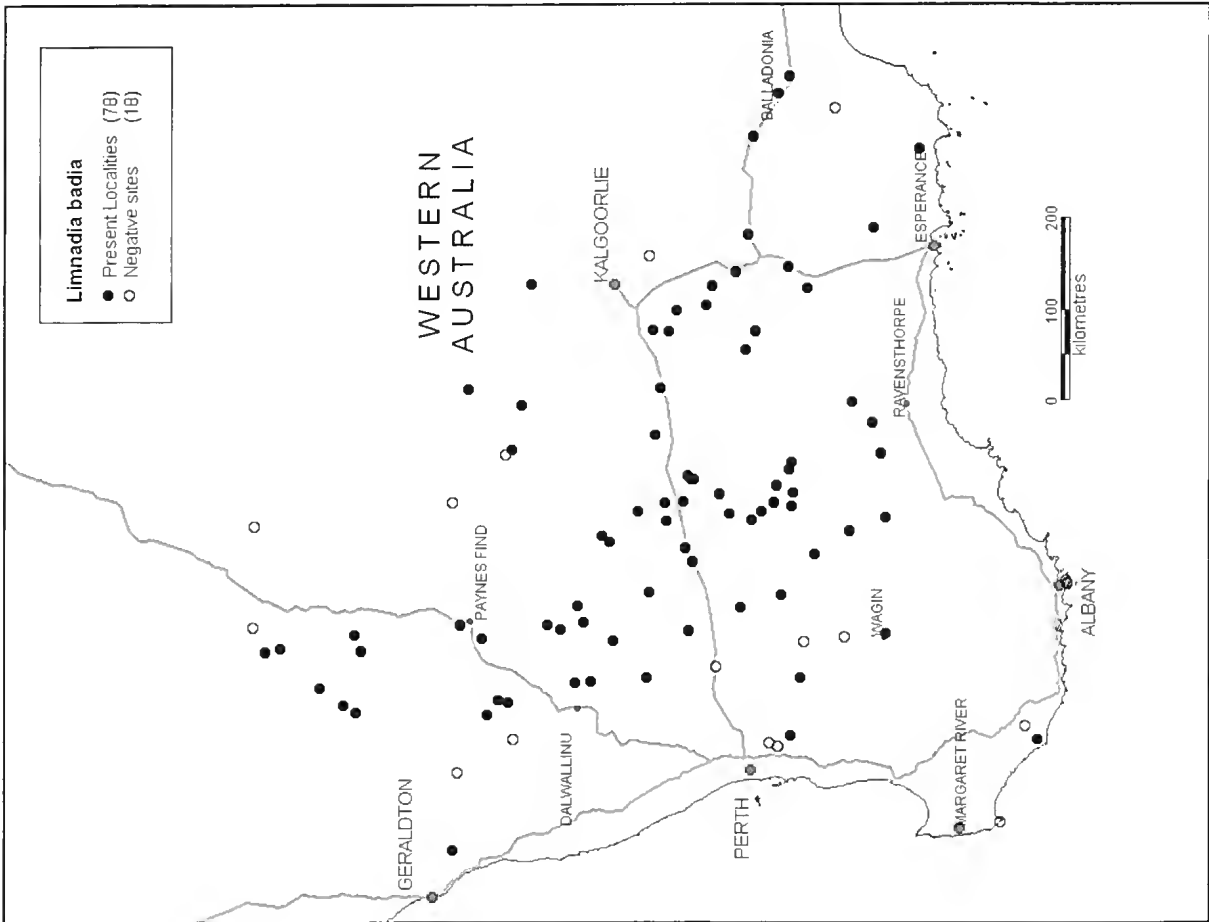
165

Figure 3. Distribution of *Limnadia badia* in south-western Australia.
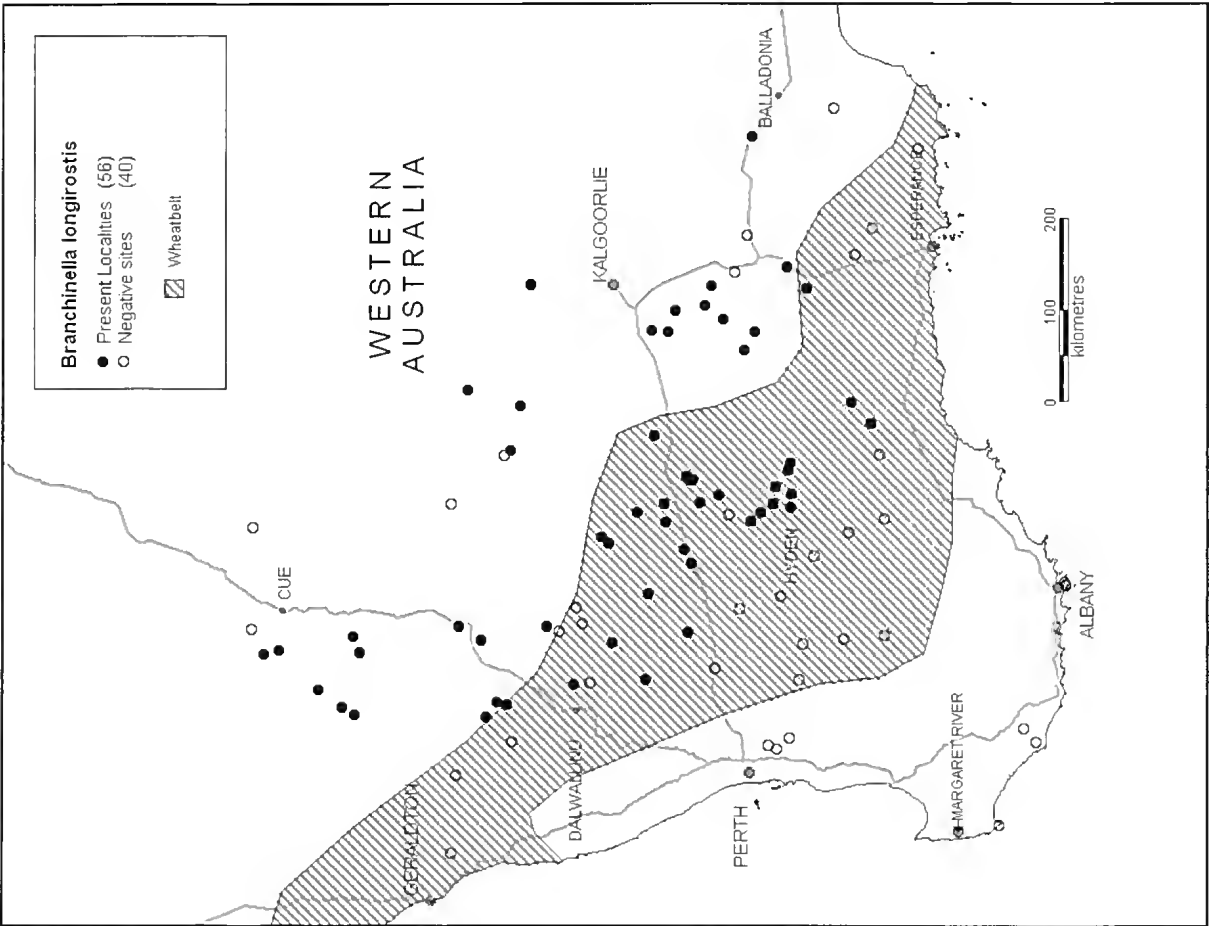

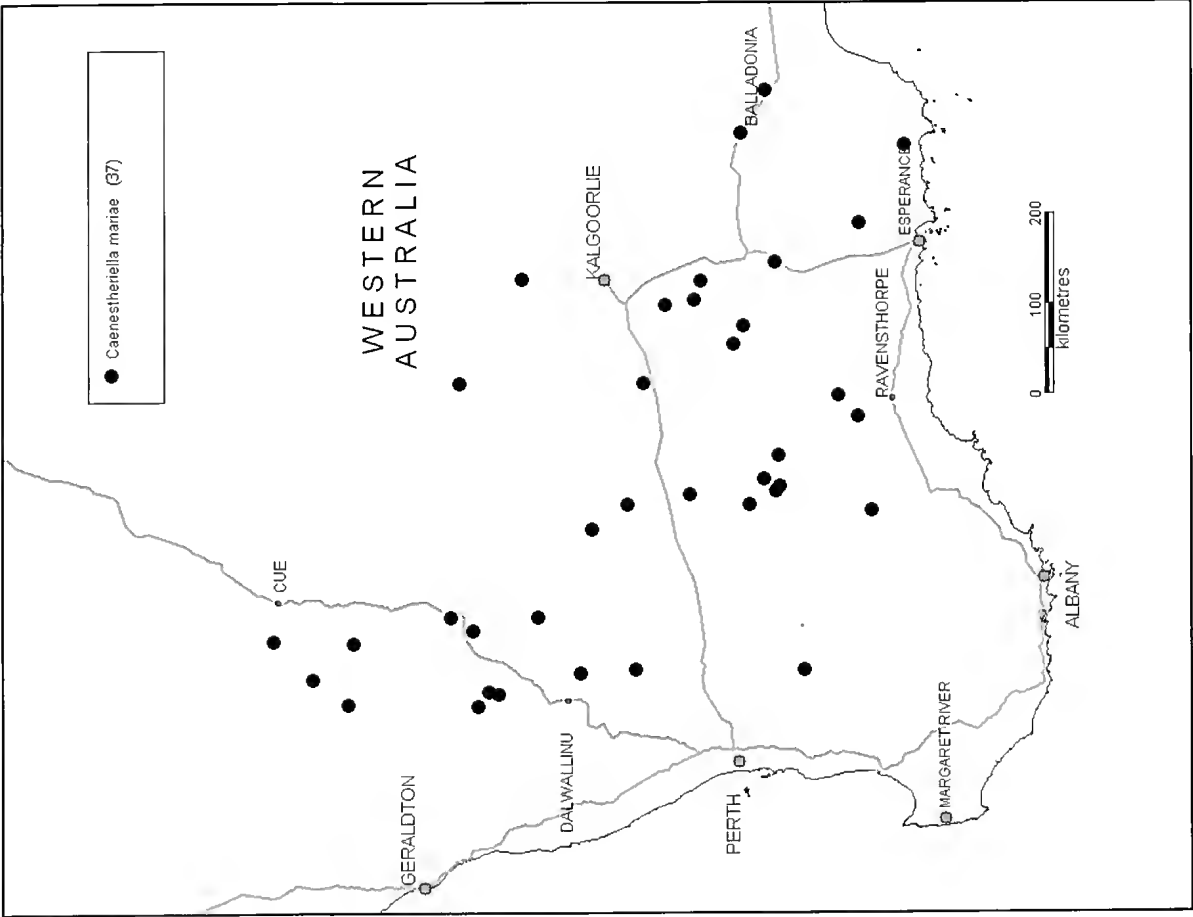**Figure 2.** Distribution of *Branchinella longirostris* in south-western Australia.

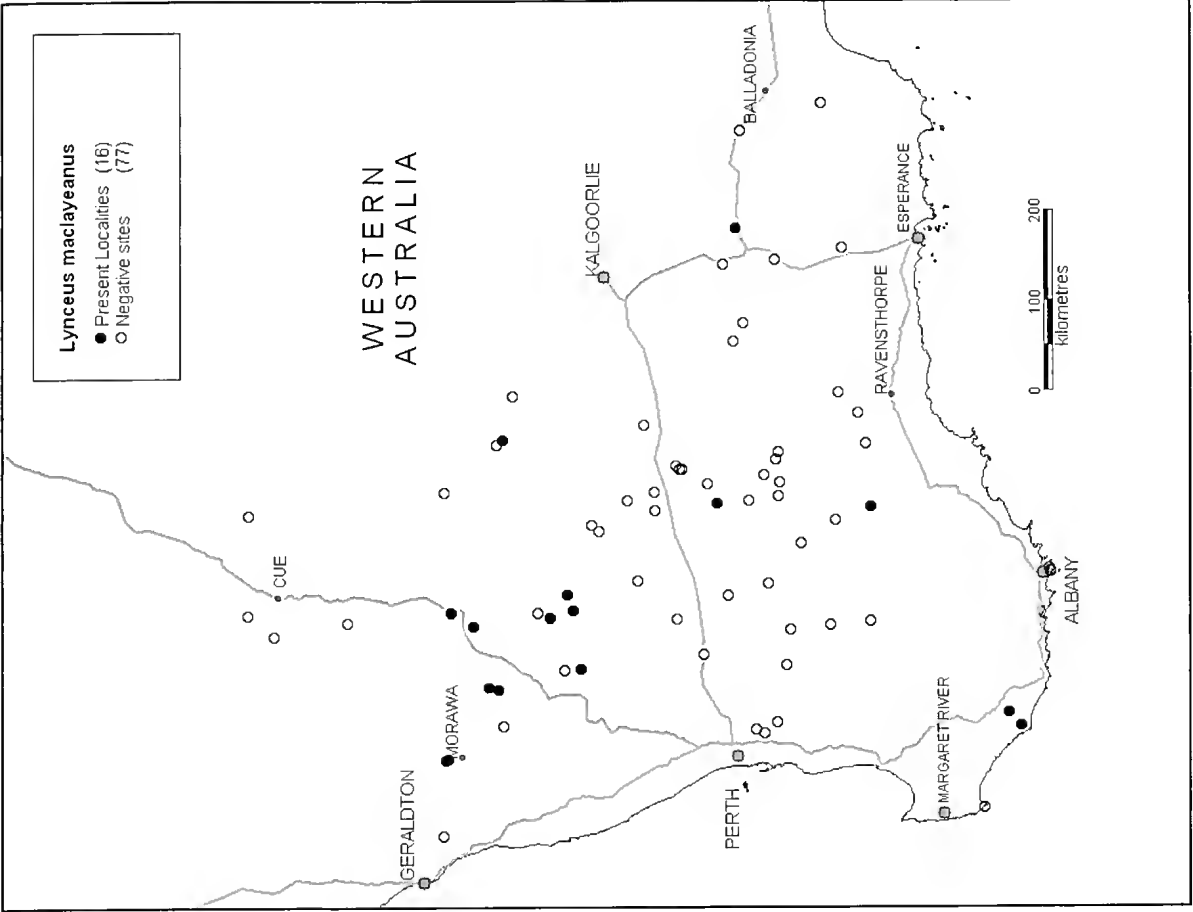**Figure 5.** Distribution of *Lynceus macleayanus* in gnammas in south-western Australia.

Figure 4. Distribution of *Caenestheriella mariae* in gnammas in south-western Australia.

longirostris lived almost exclusively in deeper pans (41% of deeper pans on rocks contained the species – range 20–100% of pools on any one rock), and hardly ever was found in shallower pans (< 1% of shallower pans on rocks with the species), never in deep pit gnammas, and only once in a large contact pool. *Caenestheriella mariae* had similar narrow habitat requirements to *Branchinella longirostris* but was not as common – 10% occurrence in deeper pans, and << 1% of shallower pans. It did not occur in deep pits and only once in a contact pool. *Limnadia badia* also was not found in deep pits and larger contact pools, but was much more common overall and more tolerant of shallower conditions [57.0% of deeper pans (range 10–100% on individual rocks), and 31.8% of shallower pools (range 10–100% on individual rocks)]. In contrast to these three species, *Lynceus macleayanus* is a deeper water specialist, being almost confined to deeper pits and larger contact pools (55.5 % of pits and 54.5% of contact pools and not in shallower pans and found in only one deeper pan).

Of the 330 occurrences of large branchiopods in 679 pools in the study area, there were 63 pools with multiple species. The most common co-occurrence (42 sites) was between *B. longirostris* and *L. badia*, and the next (7 sites) between *L. badia* and *Caenestheriella mariae*. There were seven sites with three species co-occurring. The mean number of species per pool was 0.5. Field observations suggest that the three most common species, and the ones most likely to co-occur, feed differently – *B. longirostris* filter feeds in the water column, *L. badia* feeds mainly on bottom debris and *Caenestheriella mariae* feed largely by scraping algae from hard rock surfaces.

The study of a few granite outcrops on Eyre Peninsula, South Australia, yielded only three populations of *Lynceus macleayanus* in deep gnamma pits (two on Pildappa Rock and one on Pooncarra Rock). Pans on these and the other rocks were rarely deeper than 20 cm and larger than 2 m diameter, and did not yield any large branchiopods in winter.

The above data were based on the 2003 study. The 2004 visit to many of the Western Australian sites reaffirmed occurrences, but provided a slightly different impression of relative abundance and distribution of the different species. There were more records of *Caenestheriella mariae* than in 2003 and *Triops* near *australiensis* was common on Walga and Ballan Rocks. *Branchinella longirostris* was often found in shallower pools than in 2003, explained by the pools drying because of evaporation. *B. affinis,* and occasionally *B. wellardi*, occurred in pools at the base of rocks, and at Dunn Rock, south of Newdegate, *B. affinis* occured in gnammas well away from the base, but elevated only a few metres. Contrawise, *B. longirostris* occurred only in gnammas.

Summer collections from gnammas in both Western Australia and Upper Eyre Peninsula in South Australia, have occasionally yielded *Eulimnadia dahli*. After summer storms in March 2003, some pan gnammas in the northern Wheatbelt (Appendix 1) had this species, but no other large branchiopods (M.Zofkova, pers. comm.). Pans on Corrobinnie, Peella and Pildappa Rocks on Eyre Peninsula also had populations of *E. dahli* after a storm filled pans in November 2003 (author, unpubl.

data). Indicative lengths of *Eulimnadia dahli* are ca.4–6 mm. One population of *Lynceus macleayanus* also continued to exist in November, 2003 in a large pit gnamma on Pildappa Rock, which apparently had water continuously since winter. All Eyre Peninsula pools were dry in February 2004. Following a storm in mid April, 2004, *Eulimnadia dahli* (and *B. longirostris*) were found in gnammas on King Rock (J. Hill, pers.comm.). *Eulimnadia dahli* has also been collected from Karratha Rock Hole in the Pilbara (A. Pinder, pers.comm.), and from Mt Samuel (WAM), in the far northwest and remote inland respectively, of Western Australia (Fig. 1; Appendix 1).

Other WAM records of gnamma species pertain mainly to *Lynceus* n.sp. at various sites in the central deserts of WA (including at Mt Samuel) and *Lynceus* sp. in gnammas in the limestone of the Nullabor Plain. The Mt Samuel site also harboured the anostracan *Streptocephalus* sp.

Searching by the author during 2000–2004 in selected gnammas in eastern Australia (Fig. 1) uncovered no species in granitic pans at Kooyoora State Park, via Bendigo, Victoria; *Limnadia stanleyana* in pools on sandstone at Kanangra Walls in the Blue Mountains, NSW; *Streptocephalus* sp. from a pool adjacent to granite at Byrock, NSW; *Lynceus* sp. from a rock pool in metamorphic rock at Hood Range, Currawinya National Park, southwestern Queensland; *Caenestheriella packardi* from a deep gnamma (= rockwell) on Rockwell Station, southwestern Queensland, and *Limnadia urukhai* in granitic pans near Stanthorpe, Queensland. *Limnadia stanleyana* also has been found in sandstone pools in the Budawang Mountains west of Ulladulla, NSW (M. Fielder, pers. comm.).

Discussion

Across Australia, sixteen species of large branchiopods have been recorded from gnammas (Table 2). Eleven are judged to be of low or very low frequency of occurrence, but given the right conditions some can become common at one or a few sites, e.g., *Branchinella latzi* on Uluru, NT, *Branchinella basispina* on pools adjacent to granite outcrops on the western edge of the Nullabor,WA, *Lynceus* n. sp. in deep non-granitic gnammas of the central deserts in WA, *Limnadia stanleyana* in pools sandstone mountains west and south of Sydney, NSW and *Branchinella urukhai* in the Stanthorpe area of Queensland. Others occur at more sites and are seen more often so are judged as being 'moderately frequent' in occurrence e.g., *Eulimnadia dahli* in Western Australia and South Australia, *Caenestheriella mariae* in Western Australia, *Lynceus macleayanus* mainly in granitic gnammas throughout the western inland. Two are judged as being of 'high' frequency as they are often encountered in the right season over a large area, e.g., both *Branchinella longirostris* and *Limnadia badia* in the Wheatbelt and Goldfields of Western Australia.

Many of these species are obligate gnamma inhabitants. These include *Limnadia urukhai* in Queensland/New South Wales, *Branchinella longirostris*, *Limandia badia*, and *Caenestheriella mariae* in Western Australia. It is possible that *Branchinella basispina*, *Limnadia stanleyana*, the new species of *Lynceus* in deep

Table 2

Large branchiopods in gnammas in Australia.

Species	Distribution in rock pools	Frequency of occurrence	Source
Branchinella affinis	Southern WA and southern NT	Very low	Pinder *et al.* 2000; Timms & Geddes 2003
Branchinella basispina	western edge of Nullabor Plain, WA	Low, localized	Timms & Geddes 2003
Branchinella latzi	Southern NT	Low, localized	Timms & Geddes 2003
Branchinella longirostris	Wheatbelt and Goldfields of WA	High	This study; Timms 2003
Branchinella lyrifera	NE edge of WA Wheatbelt	Very low	Pinder *et al.* 2000
Streptocephalus spp.	Cent. Australia, west. Murray-Darling Basin	Low, widespread	Bayly, 2001; Author, unpublished
Lynceus macleayanus	WA, SA, west Qld	Moderate	M. Zofkova, unpubl. data; This study; Bayly 1991
Lynceus n.sp.	Central deserts of WA	Low, localized	M. Zofkova Unpubl.data
Eulimnadia dahli	WA, Eyre Peninsula, SA	Moderate	This study
Limnadia badia	Wheatbelt and Goldfields of WA	High	This study.
Limnadia stanleyana	Sydney Basin	Low, localized	Bishop 1974
Limnadia urukhai	Granite belt of southern Qld and adjacent NSW.	Low, localized	Webb & Bell, 1979
Caenestheriella mariae	Wheatbelt & Goldfileds of WA	Moderate	This study
Caenestheriella packardi	A pit gnamma Rockwell Station; southwest Qld.	Very low, localized	Author, unpublished data
Lepiduris apus viridus	Southwest WA	Very low	Jones 1971
Triops sp near *australiensis*	Northwestern WA	Very low	This study

non-granitic gnammas of the remote inland, and the species of *Triops* in pools on Walga Rock, Ballan Rock and Karratha Rock may also qualify, but more data are needed for a confident classification. *Lynceus macleayanus* is also a gnamma specialist but not an obligate inhabitant as there are many old records in other habitats (Richter & Timms, 2005). It lives almost exclusively in deeper pools as shown in Table 1 and noted in Bayly (1997). Many species, while commonly utilizing gnamma habitat, are abundant in other habitats, including *Eulimnadia dahli, Branchinella latzi* and *B. affinis. Branchinella lyrifera* and *Lepidurus apus viridis* appear to be accidental occurrences as there is only one occurrence of each and both are common in a wide range of habitat types. Not enough is known on *Streptocephalus* spp. to know their habitat specificity. Finally, as shown by Timms and Geddes (2003), there seems to be a recent change in the dominant species on Uluru, from *Branchinella latzi* to *B. affinis.*

Western Australia has by far the most species of large branchiopods in gnammas (12) compared with the Northern Territory (3), New South Wales (3), Queensland (3), South Australia (2), Victoria and Tasmania (0). As for other aquatic invertebrates that are more speciose in southwestern WA than elsewhere *e.g., Parartemia* (Remigio *et al.* 2001), *Branchinella* (Timms 2002), cladocerans (Frey 1991; Hebert & Wilson 2000), ostracods (Halse & McRae 2004), the explanation for the west of Western Australia lies in the great age of a stable landscape. There has been no catastrophic impacts of marine inundation, little volcanism affecting the bulk of the Yilgarn Craton, or glaciation since the Permain Other contributing factors include adaptation to refugia in times of climatic stress (in this case the more reliable gnammas) and genetic isolation from eastern Australia (Pinder *et al.* 2004).

In concert with the less diverse branchiopod fauna in

Australia than in similar places worldwide (Bănărescu 1995; Williams 1981), few species occur in most Australian ganammas except those in Western Australia. By contrast southern Africa has at least six species of *Branchiopodopsis* living in rock pools (Hamer & Appleton 1996) and *Leptestheriella ineremis* (L. Brendonck, pers. com.), while in western USA and adjacent Mexico *Branchinecta lindahli, B. packardi. B. lynchi, B. coloradensis, Eubranchipus oregonus, Streptocephalus texanus, S. dorothae, Thamnocephalus platyurus, Eulimnadia texana, Leptestheria compleximanus* and *Triops longicaudatus* occur in rock pools (Baron *et al.* 1998; Belk 1991; Eng *et al.* 1990; Eriksen & Belk 1999; Graham in press; C. Rogers pers. comm.). At least some of these are gnamma specialists, including *Branchiopododsis wolfi* in southern Africa (Brendonck *et al.* 2000) but none in USA (C. Rogers pers. comm.). It is feasible that south-western Australia may have more species restricted to gnammas than elsewhere, which again probably is a reflection of the geological stability, climate variability and continuous existence of inselbergs and their gnammas over long periods of geologic time (Twidale & Campbell 1993). I emphasise geological stability because in fact the climate has been quite variable and it is probably a combination of a stable geology but instable climate that has led to high diversity – *i.e.* each climatic phase may have led to diversification but there hasn't been events like glaciation, volcanism and marine inundation (other than around the coast) to reset the fauna.

At the recent International Large Branchipod Symposium, held in Toodyay, Western Australia, in 2004 (where this paper was originally presented), a participant criticised my comment about the great age of the Yilgarn being a cause of high diversity because 'it is instability that causes speciation not stability' but I think in the case of ancient geological stability it could help preserve

diversity caused by repeated climatic variation by protecting the resulting diversity from extinction-causing catastrophic events.

It is noteworthy that among large branchiopods throughout the world, anostracans tend to dominate rock pools and notostracans are particularly scarce, despite the later's adaptations for living in such temporary environments. The contention by Main (1997, 2000) that *Triops* is a characteristic inhabitant of rock pools in Western Australia is not supported by the present data or work by Bayly (1982, 1997) and Pinder *et al.* (2000). Nevertheless, there are persistent populations of *Triops* on three rocks in the north of the state, and B. Knott (pers. comm.) contends the presence of notostracans on granite out crops in southwest Western Australia twenty years ago.

Spinicaudtan clam shrimps seem to be particularly common and diverse in Australian rock pools compared with those in southern Africa and western USA (Hamer & Appleton 1996; Baron *et al.* 1998; Brendonck *et al.* 2000; Graham in press), though this seems to contradict the statement above about relatively low diversity of large branchiopods in Australian rock pools. Six species, as well as two laevicaudatan clam shrimps are known, with differentiation across Australia. By contrast there is only one specialist anostracan (*B. longirostris*) which is restricted to an apparent centre of speciation in southwestern Australia (Timms 2002), though a few other anostracans occasionally live in gnammas.This species never occurs in nearby mud pools, and if these contain an anostracan it is likely to be the closely related *B. affinis*.

Resources in gnammas are limited and there is intense competition for them, *e.g.*, Brendonck *et al.* (2002). Co-occurrences of branchiopods seem to be less common in gnammas compared with those in other waters.Studies on North American and African gnammas rarely report co-occurrences and do not quantify them (Baron *et al.* 1998; Brendonck & Riddoch 1997; Brendonck *et al.* 2000; Eng *et al.* 1990; Eriksen & Belk 1999; Hamer & Appleton 1996). In eastern Australia no co-occurrences have been noted, but in south-western Australia 24% of pools with at least one large branchiopod had additional species. Comparative figures for all types of freshwater waterbodies with at least one large branchiopod in the wheatbelt and Carnarvon basin are 24% and 76% respectively (A. Pinder, pers.comm.). For anostracans alone there are no recorded co-occurrences in gnammas, compared with 4.9% in all wetlands of theWA Wheatbelt, 31.8% in all wetlands of the Carnarvon basin (A. Pinder, pers.comm.) and 51% of all wetlands in the Paroo in eastern Australia (Timms & Sanders 2002). For clam shrimps, there are 3.8% of gnamma sites with co-occurrences, compared with 48% among other wheatbelt sites, 11.1% of other Carnarvon sites (A. Pinder, pers.comm.) and 20.4 % of other sites in the Paroo (Timms & Richter 2002).

When there are co-occurrences in south-western Australia, the participants feed differently. Moreover there is some seasonal separation of species, with *Eulimnadia dahli* a summer species and the remainder winter-spring species. Interestingly a parallel situation is known among Chironomidae in these gnammas –

Parabornielia sp occurs in summer and *Allotrissocladius* spp. are active in winter (Bayly 1999).

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Appendix

Sites where species of large branchiopods have been found in Western Australia

Name	nearest town/locality	latitude	longitude	Branchinella longirostris*	Limnadia badia*	Caenestheriella mariae*	Lynceus macleayanus*	Other Species
Karratha Rock	Karratha	20 55	116 42					Eulimnadia dahli and Triops near australiensis-A. Pinder.
Mt Samuel	Warburton	25° 54'	125 58					Lynceus n. sp., E. dahli, Streptocephalus sp.- WAM
170 km SE Warburton	Warburton	27 00	125 05					Lynceus n.sp.- WAM
Ryans Bluff	Warburton	27 14	126 25					Lynceus n.sp.- WAM
Walloo Hill	Cue	27 15	117 26	2004	2004			
Walga Rock	Cue	27 24	117 28	2003/4	2004	2003/4		Triops near australiensis
Dalgaranga Rocks	Cue	27 46	117 01	2004	2004	2004		
Chinaman Rock	Yalgoo	28 00	116 49	2004	2004	2004		
Goolthan Hill	Yalgoo	28 07	116 44	2004	2004			
Daggar Hill	Mt Magnet	28 08	117 36	2003	2003			
Ballan Rock	Mt Magnet	28 11	117 25	2004	2004	2004		Triops near australiensis
Bilya Rock	Mingenew	29 00	115 08		M.Zofkova			
Mt East	Laverton	29 03	122 40					Lynceus n.sp.- WAM
Paynes Find Rocks	Paynes Find	29 10	117 40	2003/4	2003/4	2003	2003	
Yendang Rocks	Menzies	29 19	120 19	2004	2004	2004	2004	
Wardagga Rock	Paynes Find	29 23	117 30	2003	2003	2003		
Camel Soak	Perenjori	29 24	116 38	2004	2004	2004		
Wanarra Rock	Perenjori	29 31	116 48	2003/4	2003/4	2003/4	2003	Eulimnadia dahli - M.Zofkova
Green Rock	Perenjori	29 37	116 46	2004	2003/4	2004	2003	Eulimnadia dahli - M.Zofkova
Old Rainy Rocks	Menzies	29 44	119 37	2003	2003		2003	
Hospital Rocks	Menzies	29 50	120 07	2003	2003			
25 Mile Rocks	Menzies	29 57	121 29	2004	2004	2004		
Old Remlap Rocks	Beacon	30 02	117 38	2003/4	2003/4	2003/4		
Washington Rocks	Beacon	30 09	117 34		2003/4		2003	
Xantippe Rocks	Dallwallinu	30 17	116 58	2003/4	2003/4			
Yellari Rocks	Beacon	30 20	117 50		2003/4		2003	
Cleary Rocks	Beacon	30 23	117 39		2003/4		2003	
Petrudor Rock	Dallwallinu	30 26	116 58		2003/4	2003	2003	
Elachbutting Rock	Beacon	30 36	118 37	2003/4	2003/4	2003		Eulimnadia dahli - M.Zofkova
Yanneymooning Rocks	Beacon	30 40	118 33	A. Pinder	A. Pinder			Eulimnadia dahli - M.Zofkova
Newcarlbeon Rock	Kalannie	30 40	117 25	2004	2004			
Baladjie Rock	Bullfinch	30 57	118 53	2003/4	2003/4	2003/4		
Uberin Rock	Dowerin	30 59	116 59	2004	2004	2004		
Yarragin Rock	Trayning	31 02	117 57	2003	2003			
Weowannie Rocks	Yellowdine	31 08	119 45	2003/4	2003/4	2004		
Gnarbine Rocks	Coolgardie	31 08	120 57	2003	2003			
Boorabbin Rocks	Yellowdine	31 12	120 17		2003			
Moorine Rock	Westonia	31 13	118 59	2003/4	2003/4			
Sandford Rock	Westonia	31 14	118 46	2003	2003			
Quainine Rocks	Coolgardie	31 16	121 04	M. Zofkova				
Victoria Rock	Coolgardie	31 17	120 56	2003	2003			

Site	Nearest town	Lat	Long				Notes
Burra Rock	Coolgardie	31 22	121 11	2004	2004		
Burracoppin Rock	Merridan	31 24	118 27	2004	2004		
Yorkrakine Rock	Tammin	31 25	117 30	2003/4	2003/4		
Strawberry Rock	Southern Cross	31 27	119 17	2003	2003		
Merridan Rock	Merridan	31 28	118 18	2004	2004		
Jillbadgie Rock	Southern Cross	31 29	119 14	2003/4	2003/4		
Frog Rock	Southern Cross	31 30	119 14	2003	2003		
Dulyalbin Rock	Southern Cross	31 34	118 59	2004	2004		
Cave Hill Rock	Norseman	31 39	121 14	2004	2004		
Sunday Soak	Norseman	31 43	121 27	2004	2004		
Mt Hampton	Southern Cross	31 45	119 04	I. Bayly	I. Bayly		*Lynceus* sp.- WAM
near Madura	Nullabor Plain	31 55	127 04				
Cairn Rock	Narrembeen	31 51	118 50	I. Bayly	I. Bayly		
Coarin Rocks	Bruce Rock	31 56	117 45	2003			
25 Mile Rocks	Norseman	31 57	121 37	2003			
McDermid Rock	Coolgardie	32 02	120 43	2003/4	2003/4		*Lynceus* sp.- WAM
Nutysland Nature Res.	Nullabor Plain	32 03	126 06	2003/4			
Mt Walker	Narrembeen	32 04	118 45	2004	2004		
Buldania Rocks	Norseman	32 04	122 02	2004	2003/4	2003/4	
Newmans Rocks	Norseman	32 07	123 10	2003	2003		
Disappointment Rock	Norseman	32 08	120 56	2003/4	2003/4		
Anderson Rocks	Hyden	32 10	118 51	2003/4	2003/4	2004	
The Humps	Hyden	32 17	118 57	2004	2004		
King Rock	Hyden	32 19	119 09	2004	2003/4		
Corrigin Rock	Corrigin	32 20	117 53	2003	2003		
Afghan Rock	Balladonia	32 21	123 40	2003	2003		
Sullivan Rock	Armadale	32 22	116 15	2003			
Bushfire Rks	Hyden	32 26	119 20	2003/4	2003/4		
Wave Rk	Hyden	32 27	118 54	2003	2003/4		
McPherson Rks	Norseman	32 27	121 40	2003/4	2004		
Graham Rocks	Hyden	32 28	119 03	2004	2003		
Emu Rock	Hyden	32 28	119 25	2004	2004		
Balladonia Rock	Balladonia	32 28	123 52		2003		
Boyagin Rock	Brookton	32 29	116 55		2003		
Moir Rock	Norseman	32 39	121 25	2004	2003/4		
Jilakin Rock	Kulin	32 40	118 20		2003		
Sugg Rock	Lake King	32 58	119 39	2004	2004		
Dingo Rock	Lake Grace	33 01	118 36		2003		
Lilian Stokes Rocks	Lake King	33 04	120 06	2003	2004		
Mt Madden	Lake King	33 15	119 51	2003/4	2003/4		
Mt Ridley	Esperance	33 17	122 07		2004		
Puntipin Rock	Wagin	33 20	117 24		2003		
Dunn Rock	Newdegate	33 21	119 30		2004		
Holland Rocks	Newdegate	33 22	118 45	2003/4	2003/4	2003	
Boyatup Hill	Esperance	33 44	123 02	2004	2004		
Peak Head	Albany	35 07	117 56	D.Pirotta			

* Years in these columns refers to dated collections made by the author

The wetlands of the Lake Carey catchment, northeast Goldfields of Western Australia, with special reference to large branchiopods

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Abstract

After significant rains, many areas of the Australian arid-zone contain numerous wetlands and support a diverse aquatic fauna; an example is Lake Carey and environs. Wetlands comprise 13.6% of the Carey catchment of nearly 6000 km². Besides the large salina of Lake Carey (12.5% of catchment), there are many wetland types, including in order of total size: gypsum pans, samphire pans, salt pans, vegetated pans, red clay pans, creek pools and dams. Many of the smaller sites contain at least some water in late summer/autumn, and all are filled episodically to capacity at widely spaced intervals. Salinity is the most important factor distinguishing between sites, followed by turbidity and hydroperiod. Zooplankton and macroinvertebrates are mainly of widespread inland species, with coleopterans the most diverse, many odonatans, hemipterans and dipterans and a restricted fauna of oligochaetes, ephemeropterans, trichopterans and molluscs. The large branchiopod fauna is relatively diverse and comprises 12 anostracans in three genera (*Branchinella, Streptocephalus, Parartemia*), six clam shrimp in six genera: *Lynceus* (Laevicaudata) and *Caenestheria, Caenestheriella, Eocyzicus, Limnadia, Limnadopsis* (Spinicaudata)) and at least one notostracan (*Triops*). Almost all are widely distributed, though with many restrictions as to habitat type in the Carey wetlands. Co-occurrences within the orders, especially within the genus *Branchinella* are common.

Keywords: wetland typology, zooplankton, macroinvertebrates, Anostraca, Laevicaudata, Spinicaudata, Notostraca.

Introduction

In recent decades there have been numerous works in Australia identifying wetlands, classifying them and making inventories of their flora and fauna (*e.g.,* see McComb & Lake 1988; Pressey & Adam 1995; Roshier & Rumbachs 2004; Pinder *et al.* 2004). The majority have been strong on typology, often aided by satellite imagery and GIS, but information on flora, and especially fauna has been scant. Notable exceptions to this for the arid-zone include southern Carnarvon Basin and Wheatbelt studies in Western Australia (Halse *et al.* 2000; Keighery *et al.* 2004), the ARIDFLO program on the streams and associated lakes of the Lake Eyre Basin (Costelloe *et al.* 2004), and the Paroo wetlands in northwestern New South Wales and southwestern Queensland (Kingsford & Porter 1999; Timms 1999; Timms & Boulton 2001). In these studies extensive data are available on plants and most animal groups. The major environmental features influencing the biota of these wetlands are salinity, hydroperiod and turbidity (Timms & Boulton 2001; Pinder *et al.* 2004).

Invertebrates of these arid-zone wetlands are surprisingly diverse. The southern Carnarvon Basin has 490+ species, the southwest Western Australian wetlands have almost 1000 species and the Paroo 210+ (Halse *et al.* 2000; Timms & Boulton 2001; Pinder *et al.* 2004). Many species occur widely across the inland, but each area has its endemics, especially among the crustaceans. Large branchiopods (Anostraca, Laevicaudata, Spinicaudata, Notostraca) although recorded in most studies, have been thoroughly assessed only in the Paroo, where some 30+ species are known (Timms & Sanders 2002; Timms & Richter 2002), making it a 'hot spot' for diversity in Australia and indeed the world (Belk 1999).

In Western Australia, although detailed information on wetlands is available for large areas (see above), the goldfields of the inland are poorly known. Limited data on wetland types and their fauna are available in numerous unpublished reports to various mining companies (*e.g.,* Chaplin & John 1999; Ward 1999) and also in a few published papers, which mainly concentrate on spectacular response of some waterbirds to wetland fillings (*e.g.,* Burbridge & Fuller 1982). A general assessment of the filling-drying cycle of the small Lake Arrow near Kalgoorlie provide some data on the waterbird use of one wetland and on its invertebrates, including large branchiopods (Chapman & Timms 2004). On a wider scale, there is scant information on large branchiopods for the state, except for a broad scale taxonomic study of anostracans (Timms 2002), old records of clam and shield shrimps (*e.g.,* Wolf, 1911 on *Limnadia badia*, Linder, 1941 on *Branchinella apophystata*) and a detailed assessment of the large branchiopods in gnammas (Timms, this volume).

Lake Carey is one of many large salinas on paleodrainage systems in inland Western Australia (Van de Graaf *et al.* 1977). It is lies at 29° 00'S and 122° 20'E,

220 km ENE of Kalgoorlie and is ca 750 km² in area with a catchment of 5220 km². The lake and associated wetlands fill episodically usually after intense cyclonic rains in late summer, though lighter rains at other times may input some water into the wetlands. Like many arid-zone areas, drainage in the catchment of the lake is poorly organised so that there are innumerable wetlands following significant rainfalls. Representatives of these wetlands have been studied for two mining companies (Coleman *et al.* 2004, 2005.). This paper is based on these two studies and aims to provide a typology of wetlands of the Lake Carey catchment, an assessment of their physicochemical features and invertebrates. Special attention will be given examination of the large branchiopods of this remote and unstudied area.

Methods

The variety of wetlands in the Carey catchment was first assessed on the ground on field trips in February and April 2003 and later the variety and the extent of each wetland type was determined by analysis of a digital aerial photograph (at 450 dpi) using the program ArcView 3.2 at a scale of 1:10,000 and ER Viewer. The area was loosely divided into drainage lines and associated pans and channels and sometimes further into blocks of similar types *e.g.*, salinas, freshwater uplands, etc. The pans and channels were scored according to size and type – red clay pans, gypsum salina, salty pan, samphire pan, vegetated pan, vegetated drainage line, vegetated drainage line with channel. These were ground-truthed against known examples of each. Earthern man-made dams were easily detected on the aerial photographs and on the ground.

Analysis of the wetlands was limited by several potential generic errors:

- Falsely identifying areas as wetlands, such as wind erosion scalds and vehicle turnouts (particularly in red clays)

- Misrepresenting the salinity of the wetland – categories of salinity (gypsum, saline, fresh water) was assigned by location in the catchment.

- Underestimation of small vegetated wetlands – one wetland sampled could not be identified on the aerial photograph.

- The variety of vegetated wetlands seen on the ground could not be determined on the aerial photograph.

- It was not possible to determine the period and frequency of inundation from the aerial photograph.

Field trips were made to the study area on 15–17 February 2003, 14–17 April 2003, 10–13 March 2004 and 4–7 April 2004. Each trip was in response to significant rainfall, though some wetlands did not fill on each occasion, or were not studied for logistic reasons.

At each wetland visit the following physicochemical features were measured: depth, turbidity (with a NTU tube), conductivity, and pH (both with a TPS Model MC-81 meter). Zooplankton was collected with a net of mesh size 159 im mounted on a pole and with a rectangular

aperture 30 x 15 cm. Collections were made for 1 minute over a 10 m transect usually in the deepest part of each site (if plankton was sparse time and distance was doubled or tripled). In the laboratory, species were identified and a random sub-sample of 200 individuals counted. The remainder of the subsample was scanned for rare species and these added to the count as 0.1%. Macroinvertebrates were sampled with a rectangular dip net of aperture 30 x 15 cms and mesh size of 1 mm. This was swept through a 10m x 1m transect in two minutes to get a semiquantitative sample and sweeping continued for 15 minutes to catch uncommon species. Species present in both samples were identified using numerous different keys and the voucher specimens at the research laboratories of the Department of Conswervation and Land Management at Woodvale. Those in the 2-minute samples were enumerated, but their only presence was noted for the 15 minute samples. Large branchiopods occurred in both zooplankton and littoral macroinvertebrate samples, with most in the 15 minute macroinvertebrate net sweeps.

Mesh sizes of both nets were larger than used other survey work in Western Australia (Halse *et al.* 2000; Keighery *et al.* 2004), meaning some smaller invertebrates were probably missed, but not large branchiopods, the focus of this study.

Similarity of zooplankton and littoral assemblages at each site were analysed using multivariate techniques (Clarke & Warwick 2001). Percentage abundance of zooplankton and absolute abundance of littoral invertebrates from the two minute collections with additions from the 15 minute collections were each log transformed Data were then ordinated with non-metric multidimensional scaling using the SIMPER routine in PRIMER.

Results

The wetlands

Besides the large Lake Carey, nearly 1600 wetlands totalling 6720 ha were identified in the Carey catchment (Table 1). Gypsum pans were the most numerous (42% of total) and also by far the greatest in area (65%). Red clay pans were the next most numerous (26%), but because of their small size their combined area was small (2% of the total catchment). Vegetated pans also tended to be relatively numerous and small, particularly if the error in missing small ones is taken into account. Creek channels were not included in the calculations of areas, but if they averaged <10m wide as suggested by visual inspection of a few, then their combined areas are also small and, like the dams, contribute <0.1% of wetland areas. The non-red pans distinguished from aerial photographs could not be ground-truthed with any wetland type.

There are little data on hydroperiods for these wetlands, but field experience during 2003 and 2004 suggest the small pools in some creek channels and many dams retain water the longest and that many of the gypsum pans, salt pans and samphire pans rarely fill and when they collect a little water they soon dry. Many red clay pans and vegetated pans retain water for many weeks to a few months after significant rainfall.

Table 1

Wetlands of the Lake Carey catchment

size-frequency distribution	vegetated creek channels (km)	saline creek channels (km)	large salina	red clay pans	gypsum pans	salt pans	samphire pans	vegetated pans	non-red pans	dams	Totals
min. area 0.1 ha				377	512	80	3	72	70	20	1134
1 ha				38	99	38	14	108	30	10	337
10 ha				5	55	14	7	24	2		107
100 ha					7	4			1		12
1000 ha					3		1				4
75000ha			1								
Total numbers			1	420	676	136	25	204	103	30	1597
Total area (km or ha)	19.1	22.0	75000	125.7	4400.2	596.0	1084.3	355.2	157.0	12.0	81,720
% of Carey catchment			12.5	0.02	0.7	0.1	0.2	0.06	0.03	0.002	13.6

Wetlands studied are listed and illustrated in Coleman *et al.* (2004, 2005) and their positions are shown in Fig 1. Altogether 34 wetlands were visited, though many were not sampled on each field trip, due to logistic or time constraints, or sites being dry.

Physicochemical features

Some parameters are distinctive for the wetland types (Table 2). There was a marked dichotomy in TDS, with three saline types and the remainder fresh, though among the later, gypsum pans had a slightly elevated mean TDS. All the saline sites had clear waters, but with some elevation in turbidity in Lake Carey, while three of the fresh water sites (dams, claypans and turbid samphires) had markedly turbid waters. Most sites had alkaline waters with a pH 8.0 to 8.6, but vegetated pools usually had much lower pH. Not surprisingly dams were the deepest wetlands, though some of the gypsum pans were >0.5 m deep; by contrast claypans and saline creeks tended to be the shallowest (<0.2m).

Many sites varied between sampling trips and between years, none more so than site 2 (Standpipe Ck pool). Depending on rainfall and subsequent flow, it had characteristics of a freshwater creek pool, a samphire pan, or a salt water creek pool. Site 10, a small pool, also hardly fitted the classification – it has many physiochemical characteristics of a vegetated pool, but there was no vegetation.

Zooplankton

At least 28 species live in the Carey wetlands (Table 3); *Boeckella triarticulata*, *Mesocyclops brooksi* and *Daphnia carinata* s.l. dominated in freshwater sites, while *Meridiecyclops platypus*, *Apocyclops dengizicus*, *Diacypris* spp., *Cyprinotus edwardi* and *Repandocypris austinensis* dominated in saline waters. Some species occurred rarely, including *Latonopsis brehmi* at site 7 in both 2003 and 2004, *Moina baylyi* in Lake Carey in 2004 and *Trigonocypris globulosa* at site 22 in 2003.

Multivariate analysis of the February 2003 samples (Fig. 2a) separated saline sites (6,15,18,21) as a separate group, the turbid sites (mainly claypans, dams and turbid samphire swamps) as another (1,8,9,11,14,19, 22), the clearer water sites (included vegetated sites and freshwater creek pools) as another (3, 5, 7, 12), with site 2 as an intermediary and site 10 as an outlier. Similar analysis on a largely different set of wetlands sampled in March 2004 (Fig. 2b), point to a distinct saline group (comprising various Lake Carey sites (25,26,30,32,34) and saline creek pools (20,21), and wide spacing of the other sites, with site 2 closest to the saline sites.

Table 2

Some physicochemical features of the wetland types

Wetland type	TDS (gL⁻¹) mean ± SE	Turbidity (NTU) mean ± SE	pH mean ± SE	Depth (m)
Dams	0.20 ± 0.14	437 ± 37	8.05 ± 0.15	0.90 ± 0.10
Freshwater creek pools	0.43 ± 0.34	92 ± 80	8.56 ± 0.31	0.40 ± 0.10
Vegetated pools	0.23 ± 0.19	194 ± 71	7.43 ± 0.31	0.31 ± 0.06
Clay pans	0.20 ± 0.05	450 ± 19	8.20 ± 0.15	0.15 ± 0.04
Turbid samphires	0.32 ± 0.20	416 ± 45	8.08 ± 0.81	0.26 ± 0.13
Gypsum pans	1.5 ± 0.8	16 ± 4	8.66 ± 0.16	0.65 ± 0.18
Salt creek pools	53.3 ± 9.4	8 ± 3	8.57 ± 0.23	0.18 ± 0.04
Salt pans	47.4 ± 11.0	11 ± 4	8.43 ± 0.10	0.21 ± 0.12
Salt lake	45.3 ± 14.4	58 ± 19	8.39 ± 0.14	0.31 ± 0.03
Site 2	12.7 ± 7.6	27 ± 13	8.97 ± 0.16	0.45 ± 0.15
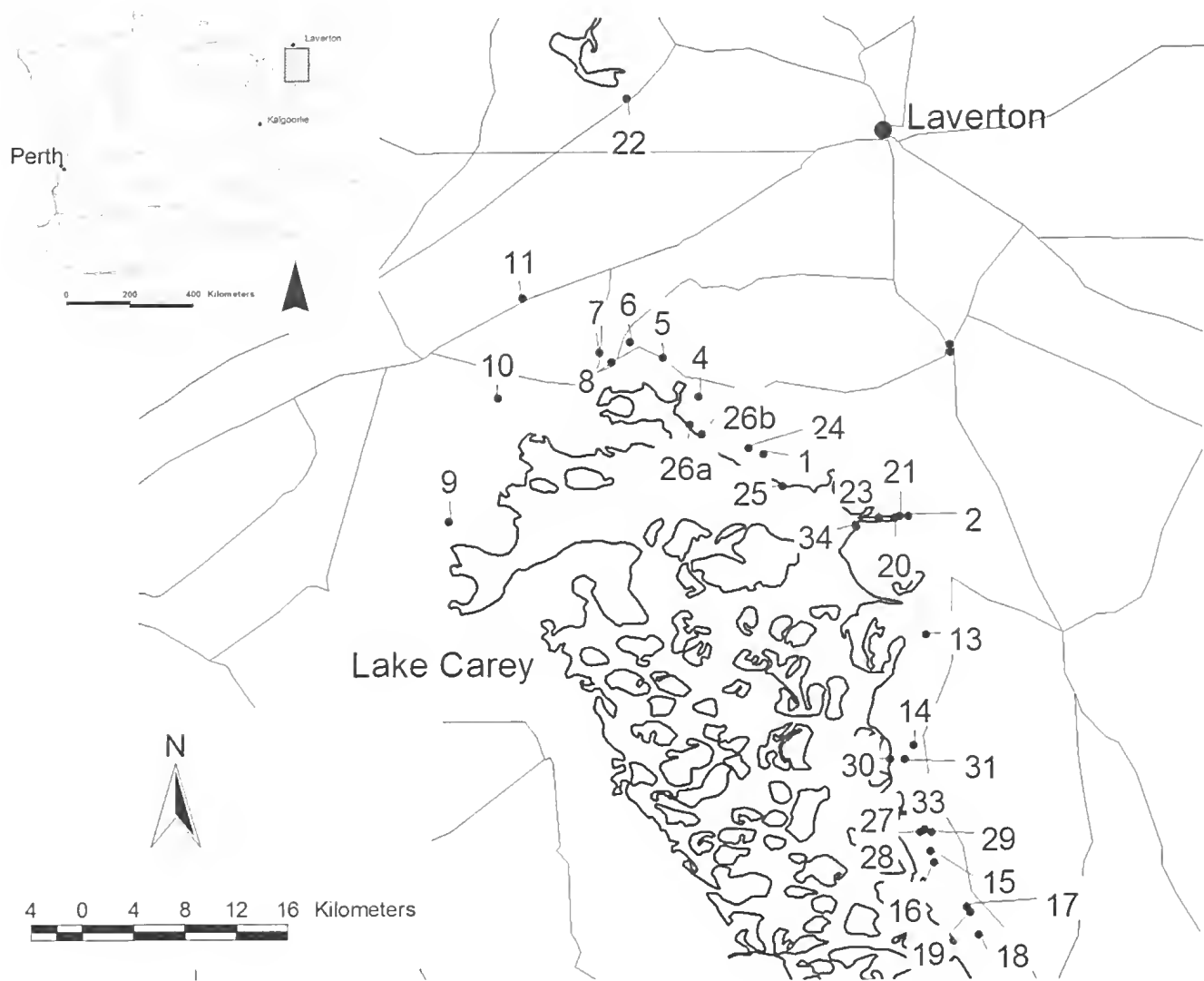
Figure 1. Map of Lake Carey and its catchment, showing the sites studied. Lake shore and islands solid lines, roads and tracks dashed. Code to sites: 1 = Ti Tree Dam, 2 = Standpipe Ck, Bindah Rd, 3 = Wynditch Ck, Mt Bold Station, 4 = a small creek, 5 = Mosquito Swamp, 6 = a salty creek, 7 = a grassed wetland near Mt Margaret, 8 = a clay pan near Mt Margaret; 9 = clay pan on Horses Head, 10 = pool near Cement Ck, 11 = a big clay pan, 12 = Wynditch Ck at road crossing, 13 = a samphire flat, 14 = Sunrise Dam, 15 = a playa South Sunrise, 16 = a playa, 17 =North Camel Playa, 18 = Camel Playa, 19 a canegrass swamp, 20 = Standpipe Ck lower, 21 = Standpipe Ck upper, 22 = The Boats, 23 Standpipe Ck mouth, 24 = Wallaby samphire flat, 25 = Wallaby Mine discharge into Lake Carey, 26 Salinaland of Lake Carey, 27 = s samphire swamp, 28 = a 'deep' gypsum lake, 29 = a samphire swamp, 30 = Old Sunrise discharge into Lake Carey, 31 = a gypsum pond, 32 = Sunrise discharge into Lake Carey, 33 = a gypsum pan, 34 = Lake Carey near Standpipe Ck.

Figure 2. Ordination diagrams of wetlands based on zooplankton assemblages. (a) February 2003 collections. (b) March 2004 collections.

Table 3

Zooplankton in Carey wetlands

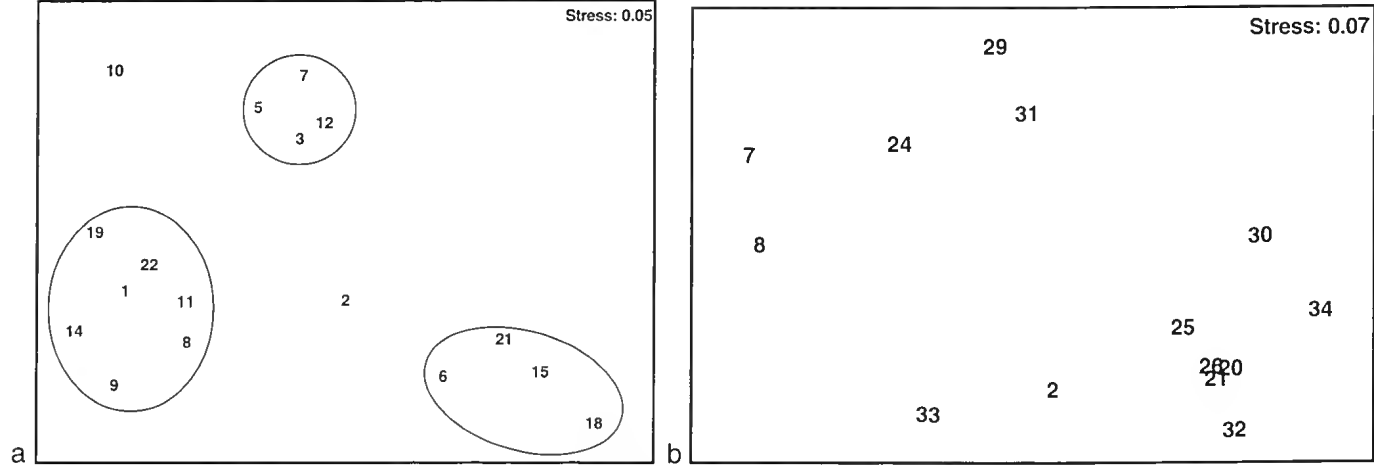| Group	Species	Feb-03 22 sites	Apr-03 17 sites	Mar-04 14 sites	Apr-04 13 sites
Rotifer	*Brachionus plicatilus* (Muller)	4	4		1
	Filinia sp.	1			
Copepoda	*Boeckella triarticulata* (Thomson)	8	9	3	4
	Boeckella sp. near *triarticulata* (Thomson)	1	2	1	
	Calamoecia near *ampulla* (Searle)	1	1		
	Apocyclops dengizicus (Lepeschkin)	3	1	3	1
	Australocypris similis Morton	9	8	2	2
	Meridiecyclops platypus Feirs	1		3	2
	Mesocyclops brooksi Pesce et al.	5	8	1	1
Cladocera	*Diaphanosoma unguiculatum* Gurney	3			
	Latonopsis brehmi Petkovski		1	1	
	Daphnia carinata s.l. King	7	5	3	3
	Daphnia near *projecta* Hebert	4	1	1	
	Ceriodaphnia sp.				1
	Moina baylyi Forro				4
	Moina micrura Kurz	11	8	2	
	Moina australiensis Sars	3	3	2	2
	Macrothrix carinata (Smirnov)		1	1	2
	Alona spp.				3
	Chydorus sp.				1
Ostracoda	*Bennelongia* spp.	1	7	3	
	Cyprinotus edwardsi McKenzie	3	5	3	3
	near *Cypridopsis* sp.	1			
	Diacypris spp.		5	6	6
	near *Heterocypris* sp.	3	1	2	2
	Repandocypris austinensis Halse & McRae	1	2	6	5
	Trigonocypris globulosa De Deckker		1		
	unknown ostracod			1	1

Macroinvertebrates except Large Branchiopods

More than 61 species of non crustacean macroinvertebrates live in the Carey wetlands (Table 4); the list would have been longer had a smaller net mesh size been used and groups such as chironomids and water mites been identified further. The most common species were *Austrolestes aridus, Micronecta* sp, *Agraptocorixa* spp., *Anisops* spp., *Berosus* spp. and *Eretes australis*. The scarcity of ephemeropterans, trichopterans, and gastropods is notable, as is the few records of many species, particularly coleopterans.

Multivariate analysis of the February 2003 samples indicate a compact saline group (6,13,15,16,17,18,20,21) and many small groups (Fig. 3a), including claypans (8,9,11), vegetated and samphire pools (5,7,19), dams (1,14), freshwater creek pools (3,4,12) with sites 2,10 and 22 as ungrouped. The March 2004 results on a largely different set of wetlands suggested a compact saline groups with distinction between Lake Carey sites (25,26,30,32,34) and saline creek sites (20,21), a grouping of gypsum pans (28,29,31,33) and with site 2 as an outlier and sites 24, 7 and 8 on the fringes of the other fresh water sites.
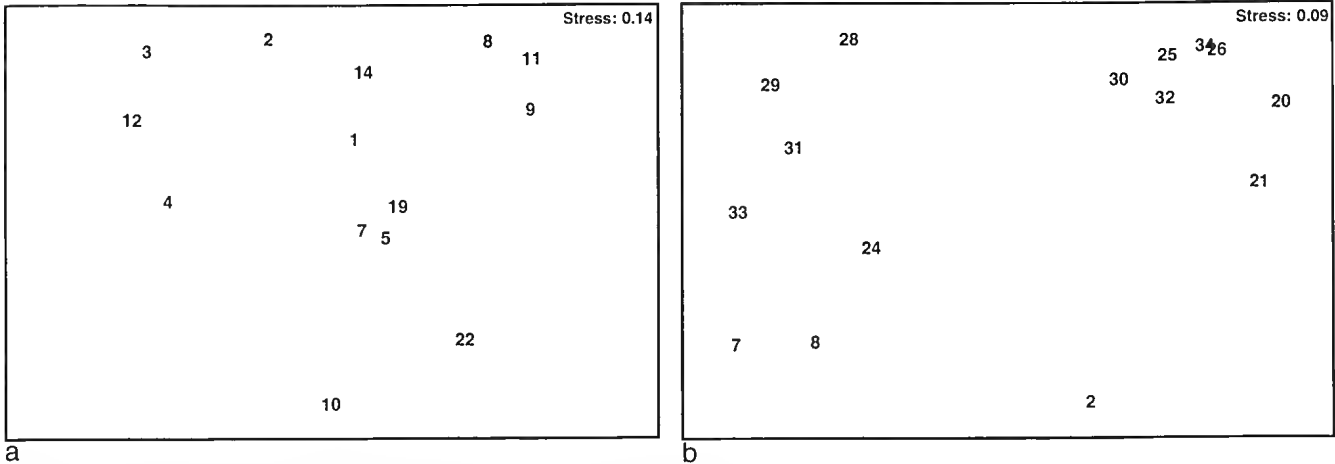

a

b

Figure 3. Ordination diagrams of wetlands based on littoral invertebrate assemblages. (a) February 2003 collections with saline sites omitted as they plot on top of each other, (b) March 2004 collections.

Table 4

Macroinvertebrates other than crustaceans in Carey wetlands

Group	Species	Feb-03 22 sites	Apr-03 15 sites	Mar-04 16 sites	Apr-04 14 sites
Oligochaeta	unidentfied species		1		
Insecta:Ephemeroptera	*Cloeon* sp.		1		
Insecta: Odonata	*Austrolestes* aridus (Tillyard)	2	6	2	4
	Xanthoagrion erythroneurum (Selys)		2		1
	Diplacoides bipunctata (Brauer)		3	1	2
	Hemianax papuensis Burmeister		1	3	3
	Hemicordulia tau (Selys)	3	5	7	9
	Trapezostigma loewii (Kaup)	2		5	4
Insecta: Hemiptera	*Micronecta* sp.	14	11	2	4
	Agraptocorixa eurynome Kirkaldy	5	1	4	4
	Agraptocorixa parvipunctata Hale	12	12	1	2
	Anisops calcaratus Hale	1	5		
	Anisops gratus Hale	14	10	4	7
	Anisops thienemanni Lundbald	8	8		3
	Anisops stali Kirkaldy	9	5	3	6
	Ansiops sp.	3			
Insecta: Trichoptera	*Triplectides australicus* Banks		2		
Insecta: Coleoptera	*Allodessus bistrigatus* (Clark)	11	6	2	3
	Antiporus gilberti (Clark)	1	1		3
	Bagous sp.	1		1	
	Berosus approximans Fairmaine	3	2		1
	Berosus australiae Mulsant & Ray	2	3	2	1
	Berosus macumbensis Blackburn	1			
	Berosus munitipennis Blackburn	3			
	Berosus nutans (MacLeay)	11	2	3	2
	Berosus spp. larvae			4	7
	Chostonestes gigas (Boheman		2		
	Copelatus ferrugineus Sharp	1	1		
	Copelatus melanarius Sharp		1		
	Cybister tripunctatus (Olivier)	2	2		
	Dineutus australis (Fabricius)	2			1
	Enochrus maculiceps (Macleay)	4	2		1
	Eretes australis (Erichson)	11	7	1	6
	Haliplus sp.	2	1		1
	Hyphydrus elegans (Montrouzier)	1			
	Hydrophilus brevispina Fairmaire	1			
	Liodessus gemellus (Clark)		1		
	Limnozenus zealandicus (Broun)	1	3		
	Macrogyrus australis Brulle				
	Megaporus howitti (Clark)	2			1
	Megaporus ?nativigi Mouchamps		1		
	Necterosoma penicillatum (Clark)	2	1		3
	Rhantus suturalis MacLeay	2	1		
	Spercheus platycephalus MacLeay		2		
	Sternolopus immarginatus Orchymont	2			
	Sternopriscus multimaculatus (Clark)	2	3		
	unidentified Sciritidae larvae	5	1		
	unidentified beetle				1
Insecta: Diptera	unidentified Chironomini	10	6	3	1
	unidentified Tanypodinae	5	10	2	3
	unidentified Tanytarsini		3	1	1
	Aedes sp.	4	3		
	Anopheles sp.			1	1
	Culex sp.	2	1		1
	unidentified Ceratopogonidae		1		2
	unidentified Tabanidae		4		
	unidentified Stratiomyidae				1
	unidentified dipteran larva (maggot)				1
Arachnida: Hydracarina	unidentified Hydrocarina	4	3	1	1
Mollusca: Gastropoda	*Glyptophysa* sp.	4	1		
	Isidorella sp.	2	3	1	1
	unidentified gastropod		1		

Table 5

Large branchiopods in Carey wetlands

Species	No. of records	TDS range (mgL⁻¹)	TDS mean (mgL⁻¹)	Turbidity range (FTU)	Turbidity mean (FTU)
Branchinella affinis Linder	14	0.02 – 1.15	0.41	5 – 500	128
Branchinella australiensis (Richters)	9	0.02 – 4.2	0.94	20 – 500	248
Branchinella denticulata Linder	1		0.12		500
Branchinella frondosa Henry	7	0.02 – 4.2	0.61	5 – 60	23.8
Branchinella halsei Timms	2	0.06 – 0.12	0.09	400 – 500	450
Branchinella nicholsi Linder	1		0.57		45
Branchinella occidentalis (Dakin)	1		0.06		500
Branchinella proboscida Henry	6	0.04 – 0.5	0.14	50 – 500	392
Branchinella simplex Linder	6	12.8 – 62	27.1	5 – 100	72.5
Streptocephalus sp.	1		1.2		30
Parartemia n. sp. g	5	8 – 51	32.5	0 – 30	11
Parartemia n. sp. x	15	22 – 105	49.5	5 – 180	54
Caenestheria dictyon (Spencer & Hall)	9	0.06 – 18.1	2.6	5 – 400	108
Caenestheriella packardi (Brady)	19	0.02 – 4.3	0.67	5 – 500	241
Eocyzicus sp.	14	0.08 – 18	5.0	5 – 500	95
Eulimnadia dahli Sars	4	0.02 – 1.2	0.33	5 – 350	294
Limnadopsis birchii (Baird)	2	0.12 – 1.2	0.66	30 – 500	265
Lynceus sp.	1		0.02		10
Triops 'australiensis' form a	14	0.02 – 4.2	0.55	5 – 500	429
Triops 'australiensis' form b	10	12.8 – 93	33.4	5 -180	76

Large Branchiopods

Nineteen species of large branchiopod crustaceans were encountered, comprising 12 anostracans, six clam shrimp (one laevicaudatan, 5 spinicaudatans) and at least one shield shrimp (Table 5). The most common anostracans were *Branchinella affinis* and *B. australiensis* in fresh waters and *Parartemia* n.sp.x in saline waters. Four species of anostracans (*B. denticulata, B. nichollsi, B. occidentalis, Streptocephalus* sp.) and two clam shrimp (*Limnadopsis birchii* and *Lynceus* sp.) are known from only one or two records each. Of the five clam shrimp species, *Caenestheriella packardi* was the most common in freshwaters and *Eocyzicus* sp. in hyposaline waters. *Triops 'australiensis'* was present as two forms difficult to differentiate except that one lives in fresh waters and the other in saline water up to 93 gL⁻¹. In addition to three saline species listed above, *B. simplex* is also a halophile (to 62 gL⁻¹)(Table 4). Almost all of the species encountered generally live in very turbid waters, notable exceptions being *B. frondosa,* and also the saline species.

Nineteen of the 67 samples (28%) had co-occurring anostracans, and 12 (16%) had co-occurring clam shrimp species. The most common combination among anostracans was the *B. simplex* and the *Parartemia* n.sp.x (7 collections), and *B. australiensis* and *B. affinis* (5 collections). One collection (site 11 March 2003) had four species: *B. occidentalis, B. australiensis, B. affinis,* and *B. proboscida*. There were two collections with three species (*B. australiensis, B. halsei,* and *B. denticulata,* and; *B. australiensis, B. frondosa,* and *B. affinis*) and 16 between two species. Among spinicaudatans the common combination was *Caenestheria dictyon* and *Eocyzicus* sp. (7 collections), and on two occasions these two were joined by *Caenestheriella packardi.*

Habitatwise, four species (*B. simplex, Parartemia* n.sp.g, *Parartemia* n.sp.x, *Triops 'australiensis'* form b) were halobionts found only in hyposaline – hypersaline waters. These included lake and saline stream sites for *Parartemia* and *Triops,* but only lake sites for *B. simplex.* *Eocyzicus* n.sp. lived in both hyposaline and fresh waters, the later including only gypsum pans and turbid samphires. Among the freshwater species with two or more occurrences, *B. probiscida* was restricted to claypans, *B. halsei* to claypans and dams, *B. frondosa* to vegetated sites and freshwater creek pools, *Eulimnadia dahli* to vegetated pools and gypsum pans, *Caenestheria dictyon* to gypsum pans and samphires, while *B. australiensis, B. affinis* and *Caenestheriella packardi* lived in a variety of freshwater sites.

Discussion

At least 107 taxa of invertebrates were collected from these Carey wetlands. The list is incomplete because some groups (*e.g.,* chironomids, water mites) were not identified or hardly studied (*e.g.,* rotifers, littoral microcrustaceans) and because a limited array of wetlands were sampled on only four field trips. By comparison, there are about 500 species in the southern Carnarvon Basin (Halse *et al.* 2000) and about 1000 in the Wheatbelt (Pinder *et al.* 2004), both in Western Australia. It is difficult to know how much to attribute the relatively low number in the Carey wetlands to inadequate study, fewer wetland sites available, smaller geographic area or harsher environmental conditions. Concerning the latter factor, a similar inland area of the middle Paroo in eastern Australia has 200+ invertebrate species (Timms & Boulton, 2001), but it is larger and better studied, while the riverine waterholes of the huge Lake Eyre basin have only 136 macroinvertebrate species but over 400 microinvertebrate species (Costelloe *et al.,* 2004).

Whatever the reasons contributing to the apparent depauperate Carey wetlands, it is certain that most of the species present are hardy ones occurring throughout much of the arid zone (Halse *et al.* 2000, Timms & Boulton 2001, Pinder *et al.* 2004,). Examples include

Boeckella triarticulata, Daphnia carinata s.l., *Branchinella australiensis, Caenestheriella packardi, Austrolestes* spp., *Hemianax papuensis, Hemicordulia tau, Micronecta* sp., *Agraptocorixa* spp., *Anisops* spp., *Triplectides australicus, Berosus* spp., and *Eretes australis.* Signficantly absent are larger crustaceans requiring permanent water (*e.g., Cherax* spp., *Macrobrachium* spp., *Holothuisiana* spp.) or at least protected places for aestivating (amphipods, isopods).

Like the Carnarvon and Wheatbelt areas (Halse *et al.* 2000; Pinder *et al.* 2004) many species are known from few individuals collected only once. Besides a few zooplankton species such as *Latonopsis brehmi, Ceriodaphnia* sp., and *Trigonocypris globulosa* (Table 2), and an array of beetles (Table 3), this list includes many large branchiopods (Table 4). Of particular interest is the absence of *Branchinella apophysata* Linder whose type locality is within the study area.

With most wetlands visited twice in each wet season, there was some variation in species composition in each as the wetland developed after filling. Notably, as expected (Hancock & Timms 2002; Timms 2001), most large branchiopods were far more common soon after filling than later and vice-versa for beetles and odonates. In cases where wetlands have been visited in different years, there was usually no significant variation in species composition. Exceptions were the variable site 2 and Lake Carey.

Lake Carey had a somewhat different fauna when up to 40cm deep in March-April and 13 to 62 gL⁻¹ (and up to 150 gL⁻¹ near one mine discharge point) than when very shallow and much more saline (ca 55 to 230 gL⁻¹) in 1998–99 (Chaplin & John 1999; Ward 1999). *Parartemia* n.sp x, cyclopoid copepods and various ostracods occurred both times, but the less saline filling had *Moina baylyi, Branchinella simplex* and *Triops 'australiensis'* and the 1998 filling had *Daphniopsis pusilla.* Episodic saline lakes varying widely in salinity are well known to have different faunas at different salinities/seasons (Williams 1990; Timms 1998), which probably points to a further differentiated fauna when the lake is subsaline/hyposaline after a major fill (Chapman & Timms 2004; Coleman, Datson & Timms unpublished data).

The 19 species of large branchiopods in Carey wetlands (Table 4) include mostly common and widespread species, but a few are of local interest. The known distribution of *Branchinella nichollsi* is extended 200 km northwards (Timms 2002); early indications that this species is halophilic (Geddes 1981) are not supported by this occurrence from a gypsum pan of fresh water and another recent record from Lake Arrow near Kalgoorlie (Chapman & Timms 2004). On the other hand, the present records extend the known upper salinity limit of *B. simplex* from 21 gL⁻¹ to 62 gL⁻¹ making it the most salt-tolerant species in *Branchinella. Parartemia* n.sp.g is the same species of a similar notation used by A. Savage (pers.comm.) and in Timms (2004); its presence in the Carey area extends its distribution inland from the Carnarvon and Pilbara areas. *Parartemia* n.sp.x is a further new species beyond the eight being described by A. Savage (pers.comm.). Presently it is known only from Lake Carey and its inflowing saline streams; this brings to four the number of *Parartemia* species known from large salinas in inland Western Australia (Timms 2004; A

Savage, pers.comm.), each with a limited geographic distribution. The repeated presence of *Triops 'australiensis'* in mesosaline and hypersaline water to 93 gL⁻¹ (Table 4) confirms that a form of *Triops australiensis* is halophilic. Previously it had been raised from this lake in hyposaline water (10 gL⁻¹)(Chaplin & John 1999). Its relationship to a superficially identical form in adjacent fresh waters is unknown.

The present study suggests a range of wetland types in the Carey catchment, with a basic divide between saline and fresh sites and among the later between turbid and clearer water sites. Highly variable hydrological patterns blur the borders between types because some sites behave differently depending on hydrological input. These same three factors, *i.e.,* salinity, turbidity, hydroperiod, are those important for invertebrate distribution and wetland assemblages in the Paroo (Timms & Boulton 2001) and are also important environmental drivers in the Southern Carnarvon district (Halse *et al.* 2000) and Wheatbelt (Pinder *et al.* 2004). Many of the wetland types, such as claypans, artificial dams, creek pools, salinas in the Carey area are distinguishable elsewhere in Western Australia (Halse *et al.* 2000; Pinder *et al.* 2004), and in other arid parts of Australia (*e.g.,* Paroo, Timms & Boulton 2001).

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Sedimentary fill of basin wetlands, central Swan Coastal Plain, southwestern Australia. Part 2: distribution of sediment types and their stratigraphy

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Abstract

The composition of wetland sediments and the variation in wetland stratigraphy across and along the length of the Swan Coastal Plain are related to geologic/geomorphic setting, regional hydrochemistry, and climate. The east-to-west variation in sediments and stratigraphy is related mainly to geomorphic setting and hydrochemistry, as reflected in the consanguineous wetland suites on the Plain, and the south-north distribution is related to consanguineous suites and to climate. Specific sedimentary sequences reside in specific consanguineous suites: for example, autochthonous sediments in the Becher Suite in the Quindalup Dunes are dominated by calcilutite. Different wetland suites within the same geomorphic setting also exhibit different sedimentary sequences: for example, in the Spearwood Dunes autochthonous sediments in the Stakehill Suite are dominated by calcilutite and peat, those in the Coogee Suite are dominated by calcilutite, while those in the Yanchep Suite are dominated by peat, diatomaceous peat, and calcilutite. Autochthonous sediments in wetlands in the Bassendean Dunes are dominated by peat and diatomite. Basins on the Pinjarra Plain are filled with terrigenous sediment (kaolinitic mud, muddy sand, and sand) and peat.

Stratigraphy of wetland fills can be vertically simple, composed of one lithology, such as peat, calcilutite, or diatomite; or complex, composed of interlayered and mixed lithologies. For many wetlands, there also is a complexity in relation to the three-dimensional arrangement of facies, *viz.*, the central facies, the basal facies and the marginal facies, and asymmetry in sedimentary fill as a result of either facies changes, or variation in thickness in sediment accumulation across a basin, or variation in the depth of the original ancestral basin. Because of the variety of processes operating along wetlands margins, such as desiccation, bioturbation, pyrogenesis, amongst others, the marginal facies of wetland sedimentary fill is the most complex ensemble of sediment types in a given wetland basin.

Information on the distribution of wetland sediments, the range of sedimentary sequences occurring across the Swan Coastal Plain in relation to geomorphic setting and hydrochemistry, and the intrabasinal stratigraphic variation vertically and laterally within single basins provide important insights into wetland sedimentary evolution, and hence wetland evolution, and provide a physical and geochemical framework to understanding hydrologic functioning and ecosystem response.

Keywords: wetland sediments, wetland stratigraphy, wetland basin, Quaternary, Swan Coastal Plain

Introduction

The stratigraphic sequences under wetlands on the Swan Coastal Plain are archives in which are encoded geologic, hydrologic and hydrochemical history, vegetation and other biotic changes, and climate changes, as preserved in their sedimentary, diagenetic, floral and faunal records. These sequences, and their relationship to wetland margins, also underpin various hydrologic processes, providing information on how a wetland functions hydrologically, and providing a basis to interpret the vegetation distribution of wetlands with respect to edaphic and hydrologic features. In these contexts we stress that it is important to develop a stratigraphic framework as a prelude to palaeo-

environmental reconstructions of wetland development, to geohydrological investigations of wetlands, and to plant ecology studies.

The importance of stratigraphy as a framework to the geohistoric, hydrologic, hydrochemical, and ecologic studies of wetlands was emphasised in a detailed study by C A Semeniuk (2006), using the young (< 4500 years) and relatively simple sedimentary sequences within wetland basins in the Becher Suite of the Quindalup Dunes. In the wetland basins of the Becher Suite there is a range of hydrological and hydrochemical responses to the geometry, thickness, composition and stratigraphy of the relatively simple basin fills, and hence response in the vegetation. Elsewhere on the Swan Coastal Plain, the sedimentary fill of wetland basins is older and more complex than those of the Becher Suite, and the wetlands contain a range of extant surface sediments and stratal

types which vary according to geomorphic setting and regional host water chemistry (C A Semeniuk 1988), and so while the general stratigraphic principles exhibited by the wetlands of the Becher Suite are relevant to these latter wetlands, the details differ. Also, generally, wetlands outside the Becher Suite are larger and hence there is more scope for intrabasinal facies variation.

A number of authors have previously documented wetland sediments and their stratigraphic expression and thickness under the Swan Coastal Plain to varying degrees of detail. The distribution of wetland sediment types and their stratigraphy, in relationship to their setting within consanguineous wetland suites and within the geomorphic units of the Swan Coastal Plain, was presented at regional scale by C A Semeniuk (1988) in order to characterise the sedimentary and stratigraphic signature of those consanguineous suites. Locally, the stratigraphy of selected wetland basins on the Swan Coastal Plain was investigated as a framework for palynological studies and palaeoclimatic reconstructions (Newsome & Pickett 1993; Pickett 1998), though these types of studies tended to concentrate on a single core as representative of the history of a given wetland basin. Basin stratigraphy for some wetlands was presented by Allen (1980) and Hall (1985) who, in their studies of local hydrogeology of wetlands, provided generalised, lithologically simplified, cross-basin stratigraphy of the wetland sedimentary fills of Lake Jandabup and Lake Mariginiup, respectively, using a number of cross-basin sampling sites to provide information on the geometric form of wetland basin fill. Megirian (1982) and C A Semeniuk (2006), to date, have provided the most detailed studies of the stratigraphy of wetland basins on the Swan Coastal Plain. Megirian (1982) studied cross-basin stratigraphy of the Bibra Lake to North Lake wetland chain in some detail, providing cross-basin information and down-profile lithologic variation to reconstruct palaeo-sedimentology. C A Semeniuk (2006) studied some 16 wetland basins in the Becher Suite, as noted above, similarly providing cross-basin information and down-profile lithologic variation to reconstruct palaeo-sedimentology, and to relate hydrology, hydrochemistry, vegetation associations, and palynology to the stratigraphic system.

While the use of a single core within a wetland basin can provide information on palaeobiological sequences with a view to unravelling biological history as a surrogate for climatic, hydrological and hydrochemical history, this approach does not address the whole-of-basin stratigraphy of wetlands, which includes wetland margin sedimentologic and hydrologic effects, basinal and marginal hydrochemistry, and cross-basin variation in biota and sedimentation patterns (Fig. 1). Given the complexity that may be present stratigraphically across a basin, and down the stratigraphic profile, researchers using information derived from a single core within a wetland to reconstruct palaeobiological sequences need to address the problem that lithological and palaeobiological changes within a given core may be representing across-basin extensions of marginal facies and biota. To fully investigate wetland stratigraphy, and to rigorously interpret the stratigraphic sequences in terms of sedimentology, palaeobiology, palaeoclimate, and palaeohydrochemistry, firstly, it is necessary to have

developed a series of wetland stratigraphic standards that can be related to their geologic, geomorphic and hydrochemical setting, and secondly, to have constructed across-basin stratigraphic relationships. Such stratigraphic information then would provide a basis on which to separate interbasin lithological variation from intrabasin variation within the same consanguineous suites, and interbasin variation between different consanguineous suites. Vertical lithologic variation in wetland stratigraphy, and its possible associated biostratigraphy, from single cores then could be more confidently assigned to one of the following: 1. intrabasin facies variation (reflecting Walther's Law; Walther 1894; Middleton 1973); 2. intrabasin factors such as hydrochemical and ecological evolution within the wetland; or 3. intrabasin lithologic (whole-of-basin) changes driven, for instance, by regional factors such as climate changes, or regional hydrochemical changes. Interbasin stratigraphic changes within and between consanguineous suites also then could be more confidently assigned to variations reflecting hydrochemical setting.

Relating surface sediment types and sedimentary fill within wetland basins to geomorphic setting and extant hydrochemistry and extant biota is the primary step in understanding the distribution of lithologic sequence(s) geographically, and should precede interpretation of stratigraphic sequences in terms of their palaeo-hydrochemical setting and palaeo-environmental setting. Further, documenting variation of interbasin wetland stratigraphy in relation to geomorphic setting ideally should form the foundation to untangling the hydrological, hydrochemical, ecological, and climatic factors that underpin stratigraphic evolution. Such an approach would place palaeobiological sequences and single-core lithological sequences for large wetland basins into a palaeo-environmental, intrabasinal, and interbasinal context.

To date, however, apart from the regional work of C A Semeniuk (1988), the distribution of wetland basin sediment types across the Swan Coastal Plain and the stratigraphic sequences within the wetlands have not been subject to a systematic and comprehensive description, and the details of their sedimentary fill remain largely unexplored. This paper is the second in a series on the sediments and sedimentary fill in wetlands across the central Swan Coastal Plain. It reports on the variety of stratigraphic sequences in basin wetlands that occur across the length and breadth of the Swan Coastal Plain, extending the detailed stratigraphic work of C A Semeniuk (2006) in wetland basins of the Becher Suite. However, as a prerequisite to describing the types and distribution of stratigraphic sequences, we describe sediment types that occur within wetland basins in relation to geomorphic setting and geographic (and hence climatic) setting. As such, this paper describes the distribution of surface sediment types in wetland basins across the central Swan Coastal Plain, and from there describes the standard stratal types within wetlands, the range of across-basin stratigraphic relationships, and the wetland basin stratigraphic diversity and internal variability. Full interpretation of the results of the stratigraphy of the wetlands presented in this paper, however, in terms of basin-specific sedimentary history,

Fence diagram, with sections oriented E-W and NE-SW, of an idealised basin with complex sedimentary fill, internal facies changes, complex margins, evidence of wetland contraction, and asymmetry in stratigraphy
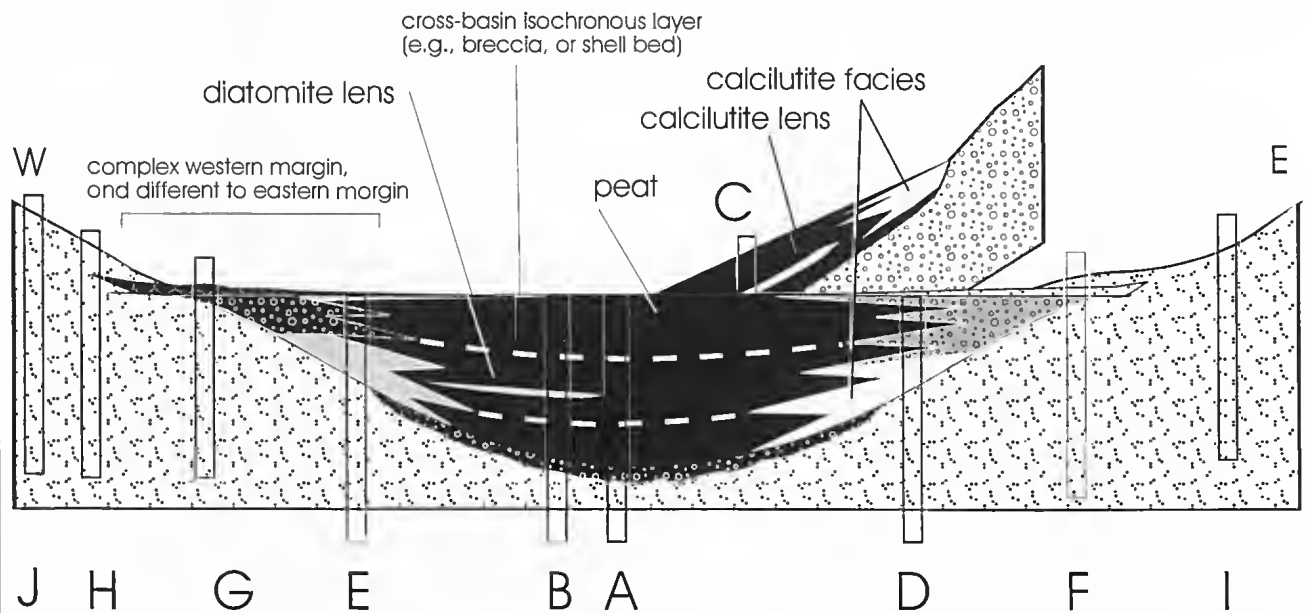
A single core at site A in the central basin: provides a simple stratigraphic sequence, and potentially an erroneously simple reconstruction of wetland history

A single core at either site A, B or C in the central basin: provides different stratigraphic sequences, and different reconstructions of wetland history

Multiple cores at sites A, B & C in the central basin: provide a more complex stratigraphic picture of intrabasinal facies changes, with documentation of intrabasinal facies changes across time and space, and more realistic reconstruction of a complex wetland history

Cores at sites D & E, in addition to those in the central basin: provide complex stratigraphic picture of intrabasinal facies changes across time and space, and variations in the marginal facies in response to fluctuations of hydrology, hydrochemistry, and biota, and hence a more complex and complete reconstruction of wetland history

The full suite of cores A to J, from central basin to upland: provides a complex stratigraphic picture of wetland facies, a context for upland-to-wetland interactions in terms of source materials, tongues and lenses of sand extending into the wetland, and a more complete picture of extant functioning and the history of the wetland in relation to hydrology, hydrochemistry, and biota; it may also help define the limit of the proto-wetland, or former wetland (from core H).

Figure 1. Cross-section of an idealised wetland showing an internally complex sedimentary fill with the various stratigraphic sequences that can be derived from single cores *versus* multiple cores. Multiple cores in transects across such basins, with focus on the wetland margins (where the process of drying and wetting is most frequent, and where the response to changes in climate, hydrology, or hydrochemistry is most marked), are the best way to unravel the wetland sedimentary history, and to relate the complex sedimentary response to wetland history in response to a changing climate, or a changing hydrochemistry.

hydrologic history, hydrochemical history, fire history, and climate changes, is beyond the scope of this paper, and will be presented in a later paper where the stratigraphic sequences are integrated with radiometric ages (Semeniuk & Semeniuk 2006, unpublished manuscript).

The geographic and environmental scope of this paper encompasses selected individual wetland basins between Gingin Brook and Bunbury. It includes wetland basins within the Quindalup Dunes in the Rockingham area (C A Semeniuk 2006), the Spearwood Dunes, Bassendean Dunes and local parts of the Pinjarra Plain (Fig. 2), but
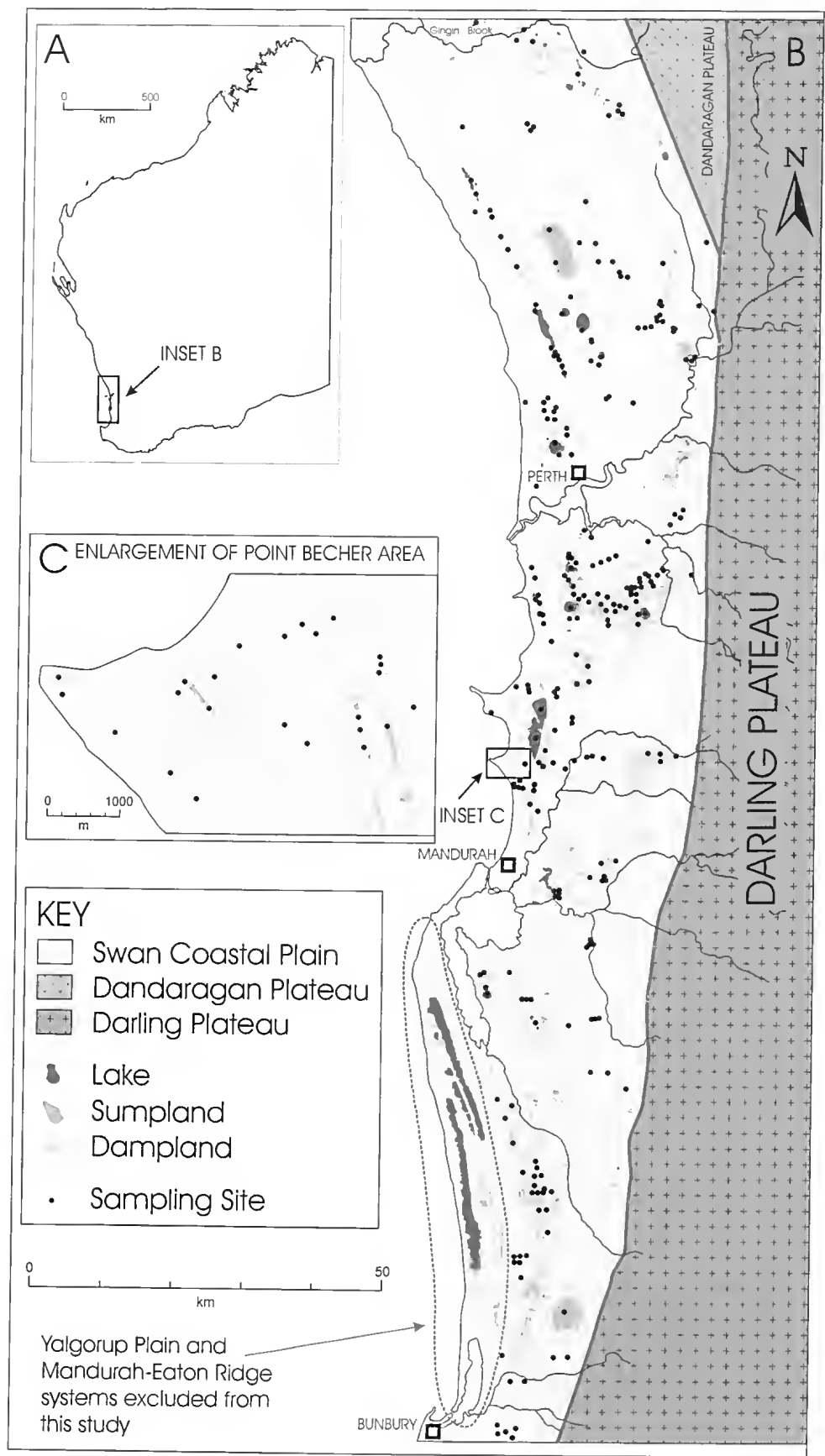
Figure 2. Location of wetlands and study sites within the central Swan Coastal Plain between Gingin Brook and Bunbury. Inset C shows details of the location of selected study sites in the Point Becher area (more detailed maps showing the comprehensive sampling locations in the Point Becher area are shown in C A Semeniuk 2006). The mapping of wetland basins as lakes, sumplands, and damplands was undertaken between 1990 and 1996 by the V & C Semeniuk Research Group, and the GIS data set is held by the former Water & Rivers Commission (now the Department of Environment and Conservation).

excludes wetlands on the Yalgorup Plain and the Mandurah-Eaton Ridge (Semeniuk 1995) which are the subject of a separate study.

The wetland classification of C A Semeniuk (1987) is used in this paper. As this paper concentrates only on basin wetlands, the relevant terms are lake (= permanently inundated basin), sumpland (= seasonally inundated basin), and dampland (= seasonally waterlogged basin). The issues of the term wetland "soil" as distinct from terms such as wetland "sediments", "stratigraphy", "stratigraphic sequence" and "sedimentary fill" have been dealt with in Semeniuk & Semeniuk (2004). In this paper, following Semeniuk & Semeniuk (2004), wetland sediments are primary infiltrational and accretionary deposits within wetland basins, and the sedimentary fill therein forms stratigraphic sequences, and thus the term "soil" is not applied to them. The boundary of a wetland basin for a lake will encompass (from wetland centre to periphery) zones of permanent inundation, seasonal inundation, and seasonal waterlogging, for a sumpland, zones of seasonal inundation, and seasonal waterlogging, and for a dampland a single zone of seasonal waterlogging. Hence, these various wetland zones are underlain by a range of infiltrational and accretionary wetland sediment deposits formed under conditions of permanent inundation, or seasonal inundation, or seasonal waterlogging (Fig. 3).

The terms for wetland sediment types follows Semeniuk & Semeniuk (2004). The term "basement" in this paper (following Semeniuk & Semeniuk 2004) refers to the floor of the ancestral wetland basin, which may be composed of Pleistocene quartz sand, Pleistocene limestone, or Holocene dune or fluvial sediments.

Sites, materials and methods

Over 250 wetland basins have been studied sedimentologically and stratigraphically for this paper (Figures 2 and 4). These include the 143 wetlands studied by Semeniuk & Semeniuk (2004), the 23 wetlands in the Becher Suite described by C A Semeniuk (2006), and some 85 additional wetlands surveyed as part of a wider regional study of freshwater sponges on the Swan Coastal Plain. Figure 2 shows the extensive occurrence of lakes, sumplands and damplands on the Swan Coastal Plain, as mapped by the V & C Semeniuk Research Group between 1990 and 1996, and the extent of sediment sampling undertaken. Not all wetlands have been sampled sedimentologically, but the sampling has covered a representative proportion of the wetland basins across the breadth and length of the Swan Coastal Plain between Gingin Brook and Bunbury, and within the various geomorphic units. In comparing the distribution of basins with respect to geomorphic setting (Figures 2, 4 and 5), note that there is a dearth of basins in the Pinjarra Plain. Most wetland basins are located in the Bassendean Dunes. However, to provide a balanced comparison of sedimentary patterns across the geomorphic units, effort was made to locate and sample a reasonable number of basins on the Pinjarra Plain. Across the whole of the study area the selection of sampling sites was based on spacing of wetlands, and accessibility.

At each sampling site, sediment samples were collected from the centre and margins of the wetlands at depths of 0–5 cm and at 20–30 cm, to characterise their surface and shallow depth sediment types. Stratigraphy of wetlands was determined along transects by examination of dewatered trenches and excavations (to 4 m) in 17 wetlands, and shallow augering in 70 wetlands (with the depth of augering, from 1 m to 5 m depth, depending on the thickness of the sedimentary fill). Additionally, in 35 of the wetlands, reverse-air-circulation coring to 30 m was undertaken (see map of locations in C A Semeniuk 1988). Augering/coring to several metres below the base of the wetland sedimentary fill into the basement sand, or limestone, and coring to depths of 30 m were undertaken to ensure that the full sequence of Holocene and any Pleistocene sedimentary fill was recorded, and to ensure that any Pleistocene wetland sequences (if present) developed *under* late Pleistocene sand sheets were intersected (*i.e.*, if indeed such sand sheets are present, separating Pleistocene and Holocene sequences).

Cliff faces provided by dewatered trenches and excavations allowed direct observation and description of wetland stratigraphy, sedimentary and biogenic structures, and sediment types. Artificial exposures were described in 12 un-named wetland basins at Osborne Park, Bullcreek, and Forrestdale, as well as in excavation trenches in Lake Gwelup, Little Carine Swamp, Lake Pinjar, and Karrinyup Road Swamp. Short cores of *in situ* sediment were obtained from a range of wetlands to study surface and near-surface sedimentary structures and micro-structures. These short cores were obtained by pushing 10 cm diameter PVC pipes, 10–30 cm long, into the substrate, retrieving them, and processing them in the laboratory. At some 46 sites, 75–100 cm long cores also were obtained, and for 6 sites with relatively deep stratigraphic sequences, cores to 5 m were obtained. In the laboratory, these cores, generally in a water-saturated state, or at least with pellicular water still present, were frozen for storage and ice-hardening. The cores later were longitudinally sliced while frozen to cleanly expose the lithology, stratigraphy, and sedimentary structures. One half was returned to frozen storage as archive material; the other half was photographed, and used in further analyses. At each wetland study site, topographic profiles and stratigraphy along transects were established by survey. Stratigraphic and topographic transects traversed adjoining upland through to wetland environments. Topographic levelling facilitated correlation of stratigraphic units within wetlands and the placement of the sedimentary fill in relation to the Australian Height Datum (AHD) for use in a later paper.

Sediments were described from cores, trenches and other excavations in terms of colour, structure, fabric, texture, and composition with stereoscopic microscope. Auger samples were similarly described, but with the omission of sedimentary structure. In the laboratory, samples returned were mounted on slides and studied by stereoscopic microscope and petrographic microscope as described by Semeniuk & Semeniuk (2004). Details of the laboratory analyses of sediments have been presented in Semeniuk & Semeniuk (2004).
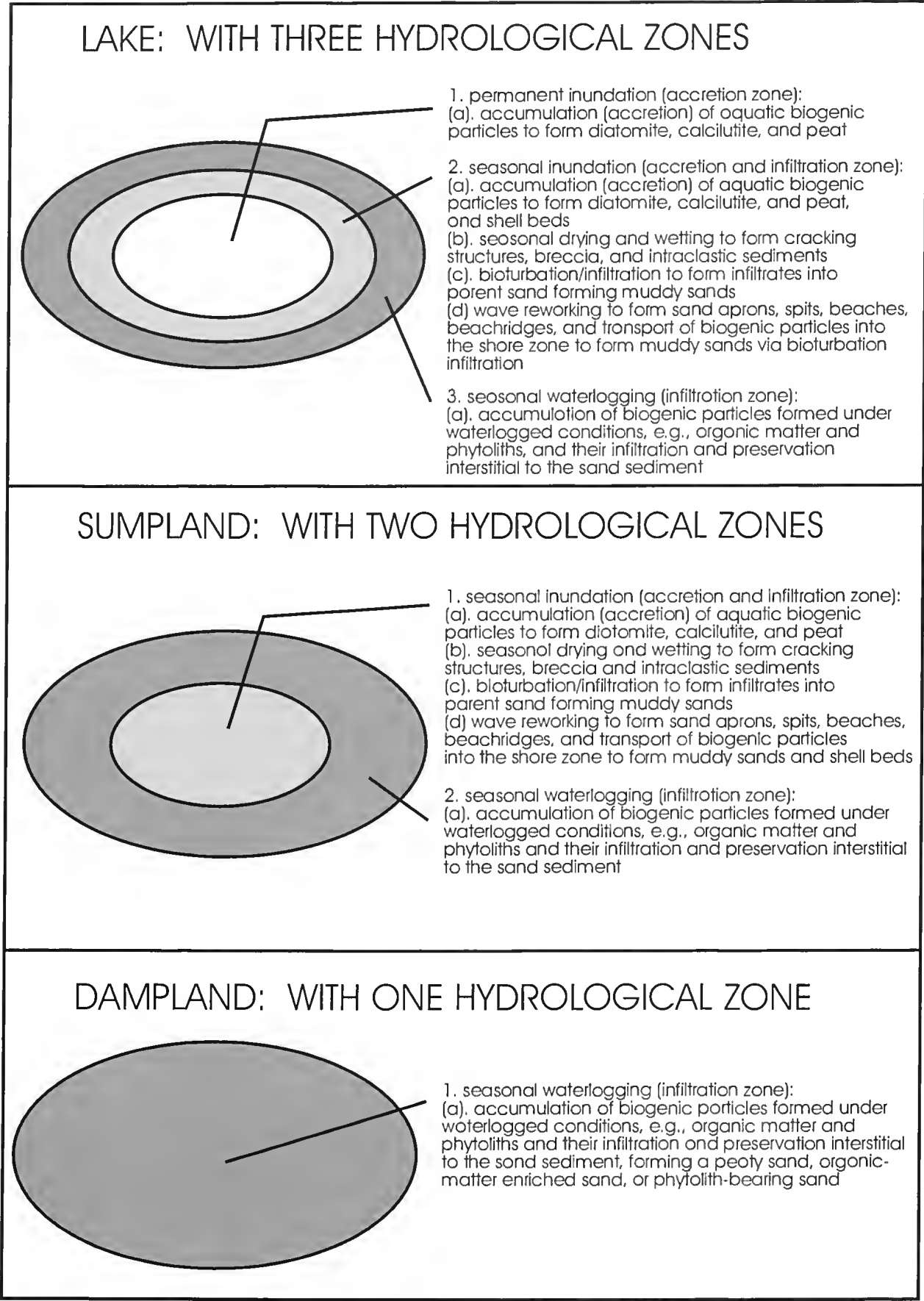
LAKE: WITH THREE HYDROLOGICAL ZONES

1. permanent inundation (accretion zone):
(a). accumulation (accretion) of aquatic biogenic particles to form diatomite, calcilutite, and peat

2. seasonal inundation (accretion and infiltration zone):
(a). accumulation (accretion) of aquatic biogenic particles to form diatomite, calcilutite, and peat, and shell beds
(b). seasonal drying and wetting to form cracking structures, breccia, and intraclastic sediments
(c). bioturbation/infiltration to form infiltrates into parent sand forming muddy sands
(d) wave reworking to form sand aprons, spits, beaches, beachridges, and transport of biogenic particles into the shore zone to form muddy sands via bioturbation infiltration

3. seasonal waterlogging (infiltration zone):
(a). accumulation of biogenic particles formed under waterlogged conditions, e.g., organic matter and phytoliths, and their infiltration and preservation interstitial to the sand sediment

SUMPLAND: WITH TWO HYDROLOGICAL ZONES

1. seasonal inundation (accretion and infiltration zone):
(a). accumulation (accretion) of aquatic biogenic particles to form diatomite, calcilutite, and peat
(b). seasonal drying and wetting to form cracking structures, breccia and intraclastic sediments
(c). bioturbation/infiltration to form infiltrates into parent sand forming muddy sands
(d) wave reworking to form sand aprons, spits, beaches, beachridges, and transport of biogenic particles into the shore zone to form muddy sands and shell beds

2. seasonal waterlogging (infiltration zone):
(a). accumulation of biogenic particles formed under waterlogged conditions, e.g., organic matter and phytoliths and their infiltration and preservation interstitial to the sand sediment

DAMPLAND: WITH ONE HYDROLOGICAL ZONE

1. seasonal waterlogging (infiltration zone):
(a). accumulation of biogenic particles formed under waterlogged conditions, e.g., organic matter and phytoliths and their infiltration and preservation interstitial to the sand sediment, forming a peaty sand, organic-matter enriched sand, or phytolith-bearing sand

Figure 3. The broad sedimentary setting of the various zones of a wetland basin (as a lake, sumpland, or dampland) in relation to permanent inundation, seasonal inundation, seasonal waterlogging, and the simplified outline of the types of sediments accumulating in terms of lithology and their status as infiltrational or accretionary deposits. This diagram focuses on intrabasinally generated biogenic sediments rather extrabasinal sediments. Muddy sand in this diagram refers to peaty sand, calcilutaceous muddy sand, or diatomaceous muddy sand (see Semeniuk & Semeniuk 2004).
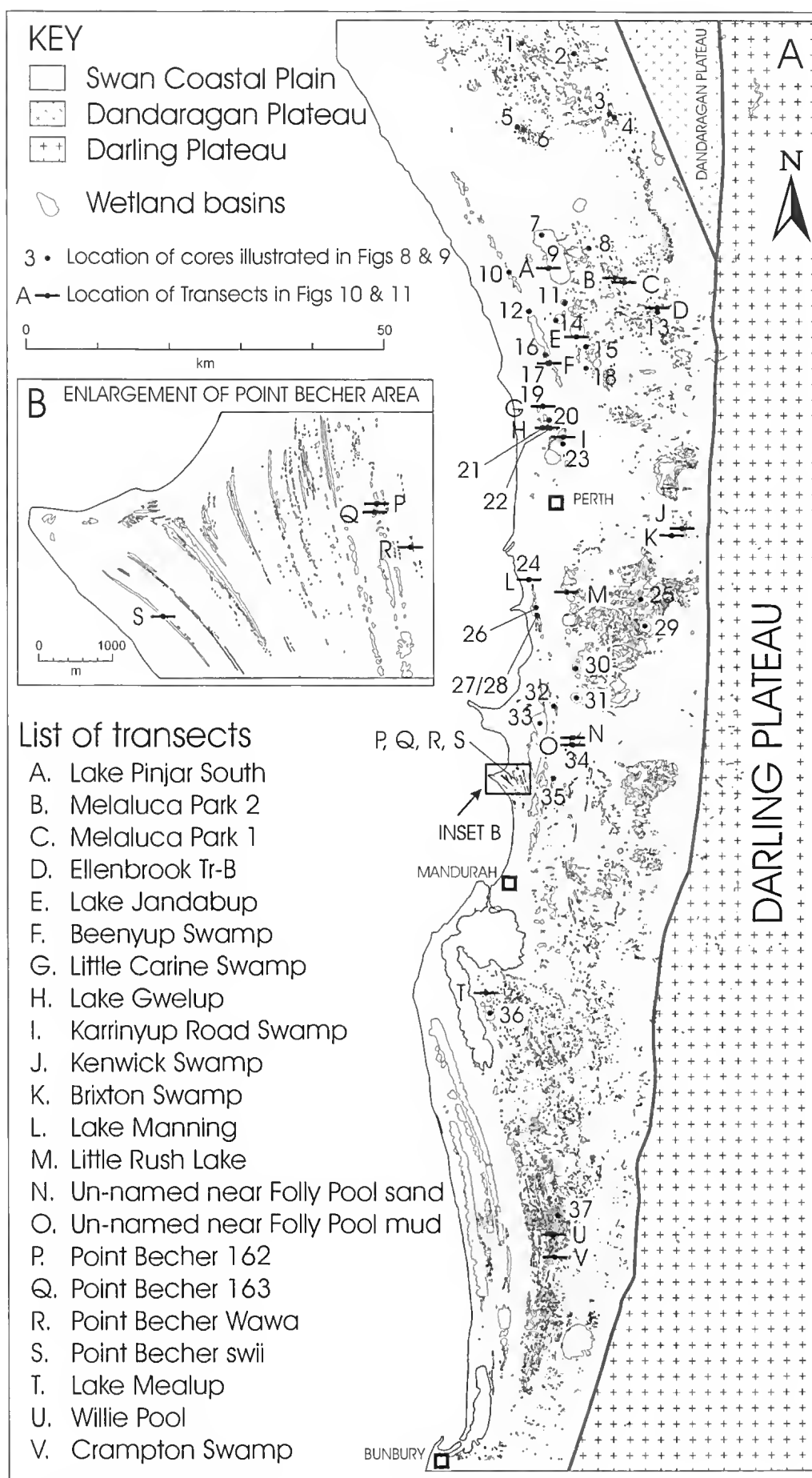
KEY

- ☐ Swan Coastal Plain
- ⬚ Dandaragan Plateau
- ⊞ Darling Plateau

- ◌ Wetland basins

- 3 • Location of cores illustrated in Figs 8 & 9
- A ⊢• Location of Transects in Figs 10 & 11

0   50
km

B   ENLARGEMENT OF POINT BECHER AREA

0   1000
m

List of transects

- A. Lake Pinjar South
- B. Melaluca Park 2
- C. Melaluca Park 1
- D. Ellenbrook Tr-B
- E. Lake Jandabup
- F. Beenyup Swamp
- G. Little Carine Swamp
- H. Lake Gwelup
- I. Karrinyup Road Swamp
- J. Kenwick Swamp
- K. Brixton Swamp
- L. Lake Manning
- M. Little Rush Lake
- N. Un-named near Folly Pool sand
- O. Un-named near Folly Pool mud
- P. Point Becher 162
- Q. Point Becher 163
- R. Point Becher Wawa
- S. Point Becher swii
- T. Lake Mealup
- U. Willie Pool
- V. Crampton Swamp

Figure 4. Study sites where data are used in the illustrations of cores and transects in this paper.

Wetlands on the Swan Coastal Plain and their geologic, geomorphic, hydrochemical, and consanguineous setting

Geologic and geomorphic setting

The Swan Coastal Plain, which is host to a variety of wetlands, is the Quaternary surface of the Perth Basin (Playford *et al.*, 1976), and comprises distinct large-scale landforms largely arranged subparallel to the Darling Scarp, or subparallel to the coast, or are associated with major rivers. These landforms correspond to the main Quaternary sedimentary formations in the region (Woolnough 1920; McArthur & Bettenay 1960; Playford *et al.*, 1976; McArthur & Bartle 1980a,b; C A Semeniuk 1988; Semeniuk & Glassford 1987, 1989; Semeniuk *et al.*, 1989; Geological Survey of Western Australia 1990; Semeniuk 1995). The main units from east to west are (Fig. 5):

- Pinjarra Plain: flat to gently undulating alluvial fans fronting the Darling Scarp and Darling Plateau (underlain by sand, laterite, and Precambrian rocks), as well as floodplains and various sized channels; underlain by the Guildford Formation (clay, laterite, sand, muddy sand);

- Bassendean Dunes: undulating terrain mostly of low degraded dunes (varying in relative relief from 20 m to almost flat), and interdune flats and basins; underlain by the Bassendean Sand (quartz sand) of Pleistocene age;

- Spearwood Dunes and Yalgorup Plain: large-scale, linear, near-continuous subparallel ridges (up to *circa* 60 m relief) and intervening narrow and steep-sided depressions, or of narrow plains; underlain by Pleistocene limestone (aeolianite and marine limestone) blanketed by quartz sand; and

- Quindalup Dunes: Holocene coastal dunes, beach ridge plains, tombolos and cuspate forelands; underlain by quartzo-calcareous sand.

In the southern part of the study area, there is the Yalgorup Plain (underlain by limestone and quartz sand, and equivalent to the Spearwood Dunes), which is separated from the Bassendean Dunes by the Mandurah-Eaton Ridge, a ridge of moderate relief underlain by quartz sand (Semeniuk 1995; and Figures 2 and 5).

In these settings, there are four main lithologic/stratigraphic units that either adjoin or underlie wetlands: 1. Pleistocene yellow to white quartz sand; 2. Pleistocene limestone; 3. Holocene quartzo-calcareous sand; and 4. Pleistocene to Holocene fluvial sand, muddy sand, and mud.

The array of sampling sites for this study, within the framework of the geomorphic units to illustrate the extensive sampling along the length and breadth of the Swan Coastal Plain in relation to these geomorphic units, is shown in Figure 5.

Hydrochemical setting

Most of the Swan Coastal Plain is underlain by an unconfined groundwater body that resides in a variety of aquifers, which are variable in lithology, depending on geological setting. The aquifers include quartzo-calcareous sand, calcareous sand, limestone, interlayered limestone and quartz sand, quartz sand, muddy sand, and interlayered sand, muddy sand and mud, corresponding to the formations of Safety Bay Sand, Becher Sand, Tamala Limestone and other "coastal limestones", Bassendean Sand, and Guildford Formation (Playford *et al* 1976, Semeniuk & Searle 1985; Semeniuk 1995).

Groundwater is mostly fresh, with salinities ranging from < 250 ppm to 1000 ppm, though locally there are tongues and lenses of groundwater with salinity 1000–2000 ppm and limited occurrences with salinity > 2000 ppm (Davidson 1995).

The hydrochemistry of the groundwater will have an influence on wetlands in its effect on biota, and its effect on sediments and diagenesis, and thus in this context it is important to develop a framework of hydrochemistry within which to deal with wetland sedimentation and stratigraphy. Table 1 summarises the hydrochemistry of the Swan Coastal Plain in relation to landscape setting with respect to salinity, pH, and Ca, Si, and Fe content. These data are not chemical parameters of waters in wetlands themselves but of the groundwater of the terrain in which wetlands may reside. Groundwater pH, where alkaline, provides an indication of how much $CaCO_3$ has been dissolved from the aquifer lithology; acidic waters signal waters residing in aquifers of low carbonate content. The quartz sands of the Swan Coastal Plain often are Fe-stained, with coatings of Fe oxides (as yellow goethite and red haematite), and Fe pigmentation of the clay and silt coating around the quartz grains, resulting in yellow colouration of the sand in the region (Glassford 1980; Semeniuk & Glassford 1989; Glassford & Semeniuk 1990). Acidic waters disaggregate the coatings and mobilise this Fe into solution (Semeniuk &

Table 1

Summary of selected telluric hydrochemistry of groundwater of the Quindalup Dunes, Spearwood Dunes, and Bassendean Dunes

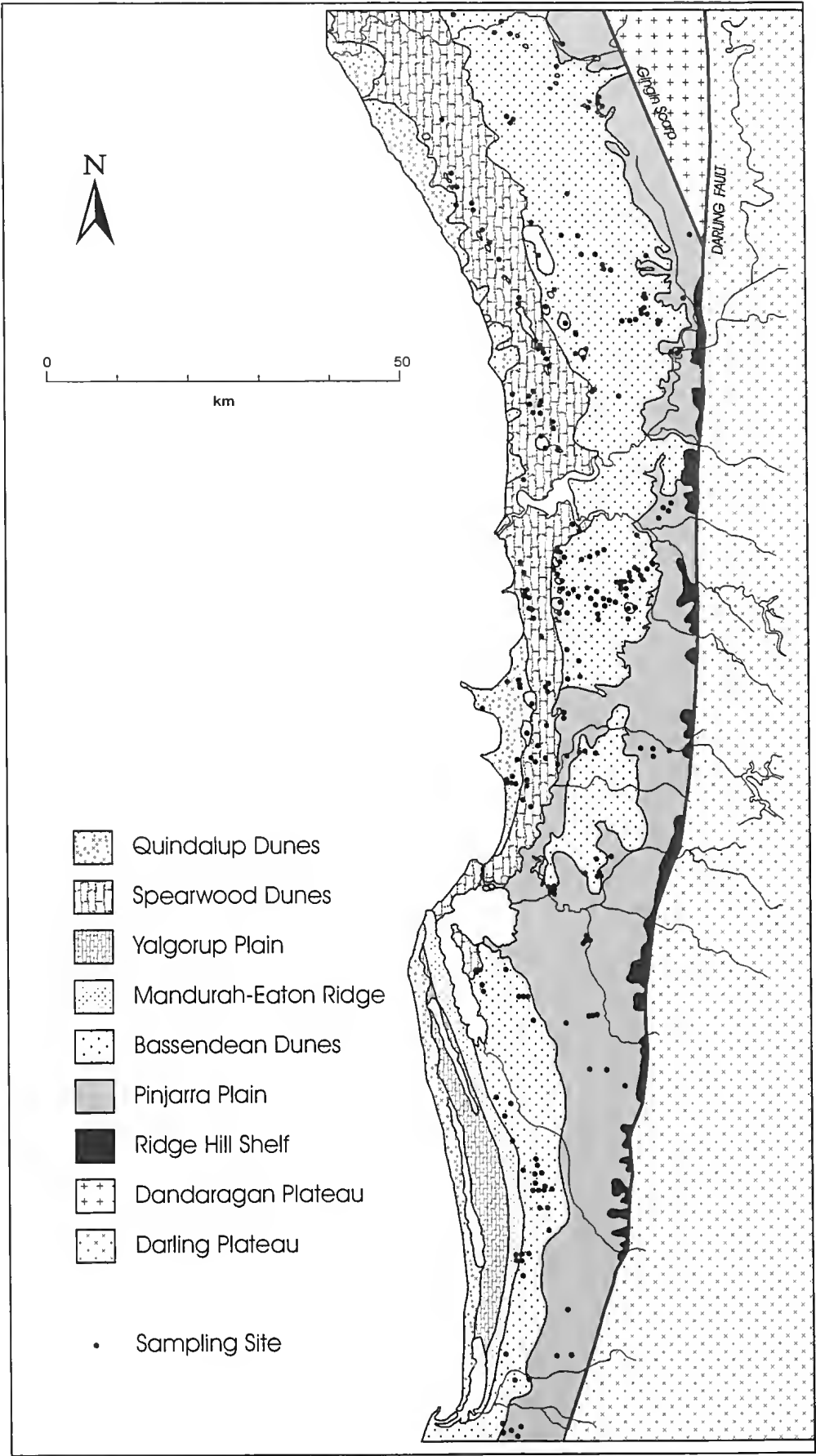| Geological/geomorphic setting	Salinity (ppm) mean (& range)	pH mean (& range)	Ca (ppm)	SiO$_2$ (ppm)	Fe (ppm)	No of samples
Safety Bay Sand (Quindalup Dunes)	446 (300–1100)	7.9 (6.8–8.8)	32	15	0.2	110
Tamala Limestone (Spearwood Dunes)	420 (290–900)	6.3 (6.1–7.2)	53	14	0.5	96
Bassendean Sand (Bassendean Dunes)	340 (70–1750)	5.5 (4.3–7.0)	9	11	0.7	144

Figure 5. The geomorphic framework of the central Swan Coastal Plain (modified after McArthur & Bettenay 1960, with information on the Yalgorup Plain and Mandurah-Eaton Ridge from Semeniuk 1995) with overlay of location of study sites to illustrate extensive sampling in relation to the various geomorphic units.

Semeniuk 2004), such that groundwaters that are slightly acidic and in contact with yellow sand will have higher Fe content, and alkaline waters will have relatively lower Fe content. Similarly, alkaline waters are silica dissolving, and acidic waters are silica precipitating, hence the pH of groundwater will relate to the content of silica in solution (Correns 1950; Krauskopf 1956; Okamoto *et al.* 1957). There is more SiO_2 in solution in groundwaters of carbonate terrains with alkaline water than in terrains of quartz sand with acidic waters, as alkaline waters favour the solution of silica, even though the content of silica (as sand grains) is higher in the latter terrains. The Ca content is a measure of how much calcareous material has been dissolved from host rocks and carbonate-bearing sands into the groundwater, and thus is a measure of the telluric nature of the groundwater. Consequently, the Ca, Fe, and Si content of groundwater can be used as a measure of its telluric nature, and a measure of how much the lithology of the aquifers determines the chemical nature of ground waters before they have reached wetlands.

These water quality parameters show that source waters that will enter wetlands are generally of low salinity. If they are telluric in character deriving from calcareous hosts they will have relatively elevated Ca content, and neutral to alkaline pH. If they are deriving from quartz rich terrains they will be acidic, and with relatively low Ca content.

In contrast, rainwater data presented by C A Semeniuk (2006) on the Quindalup Dunes in the Becher Point area, collected over a number of years, show its salinity is 99 + 116 ppm 0.5 km from the coast, and 114 + 86 3–4 km from the coast. Its Ca content is as low as 6.6 ppm and ranges up to 9.5 ppm, equivalent to the Ca content of groundwater in the Bassendean Sand. Its Fe content is 0.03 ppm, and SiO_2 content is 1.24 ppm. Data from 80 samples collected daily at Floreat over 1996–1998 (Rich & Semeniuk, unpublished MS) show the salinity of rainwater to be 299 + 227 ppm (range 30 ppm – 980 ppm), its Ca content to be 1.6 + 1.5 ppm, and its Fe content to be 0.02 + 0.02 ppm.

The low cation and SiO_2 content of rainwater in contrast to the higher Ca, Fe and content of groundwaters (correlative with the various aquifer settings) show the effect of aquifer geochemistry on the hydrochemistry of telluric waters.

Hingston & Gailitis (1976) provide data on the salt content of rain water in the southwest of Western Australia, with study sites relevant to this paper at Yanchep, Floreat, Perth, Harvey, and Bunbury. Their results, however, are not directly comparable to those of this paper mainly because they have converted salt content (whether total salt, Cl, or specific cations) to values of kg/ha.

Some of the important aspects of hyrochemistry in relation to wetlands, particularly in their influence on biota, sediments and diagenesis, are: 1. salinity (which effects selection, elimination, and productivity of biota, and hence generation of biogenic sedimentary particles); 2. the Ca-and-HCO_3 content (which firstly effects the availability of Ca and HCO_3 ions and hence the rate of acquisition of carbonate minerals by biota, and secondly, influences diagenesis); 3. Si content (which influences diatom occurrence); 4. pH (which influences biota, long term residency time of annually generated fine-grained carbonate particles and fine-grained biogenic silica particles, and Fe hydrochemistry and geochemistry); and 5. water colour (*e.g.*, tannin content, which influences benthic and planktonic biota, and which may also regulate other aspects of water chemistry and microbiota). Components such as NO_3 and PO_4 also were important aspects of hydrochemistry in their influence on the productivity of biota and hence generation of sedimentary particles, but it is now difficult to assess the importance of these chemical species in determining distribution of sediment types because there has been major anthropogenic nutrient enrichment of wetlands from urbanisation and agricultural development, which has confounded any original patterns.

Meteoric waters, derived from oceanic air masses and containing salt spray, essentially mirror the chemistry of diluted seawater, and hence largely reflect its cationic ratios, while water originally derived from meteoric sources residing for some time in chemically distinct aquifers carries the signature of those aquifers as telluric waters (Table 1). Waters residing in wetlands, regardless of whether they derive from meteoric sources, or initially carry telluric signatures, commonly reflect the processes that operate in wetlands. For example, wetlands with perched meteoric water (and where there is little vertical throughflow such that evaporation is dominant over meteoric input and groundwater throughflow) tend to contain brackish to saline water. Wetlands underlain by carbonate sediments have waters enriched in Ca ions, as the surface waters chemically equilibrate with the sediments (cf. C A Semeniuk 2006). Wetlands underlain by peat tend to have tannin-stained, acidic waters, and wetlands underlain by diatomite (usually with organic matter enriched surface layers) also tend to have tannin-stained, acidic waters.

Phreatic waters under wetlands, below the zone of water table fluctuation, have a variable hydrochemistry, as determined by the geochemistry of each wetland sedimentary fill, and the complexity of the lithological layering in wetland sedimentary sequences (C A Semeniuk 2006). The hydrochemistry of downward percolating groundwaters has little influence on sediment generation within wetlands but would have an effect on shallow-depth wetland sediment diagenesis. For wetlands partially maintained by local artesian or subartesian water, the chemical perturbations and chemical signature effected by subsurface wetland sediments have some influence in determining wetland surface water chemistry.

To deal with the complexities of the chemical variation and evolution of surface and groundwater within and around wetlands, as discussed above, the hydrochemistry of waters within wetlands and groundwater under the Swan Coastal Plain in relationship to wetlands is categorised, in this paper, into three spatial fields relative to a wetland basin:

Type 1: groundwater *within* the geological/ geomorphic setting where the wetland resides; this potentially reflects the hydrochemistry of the source waters for the wetlands (where local artesian and subartesian waters are not involved), and will be one
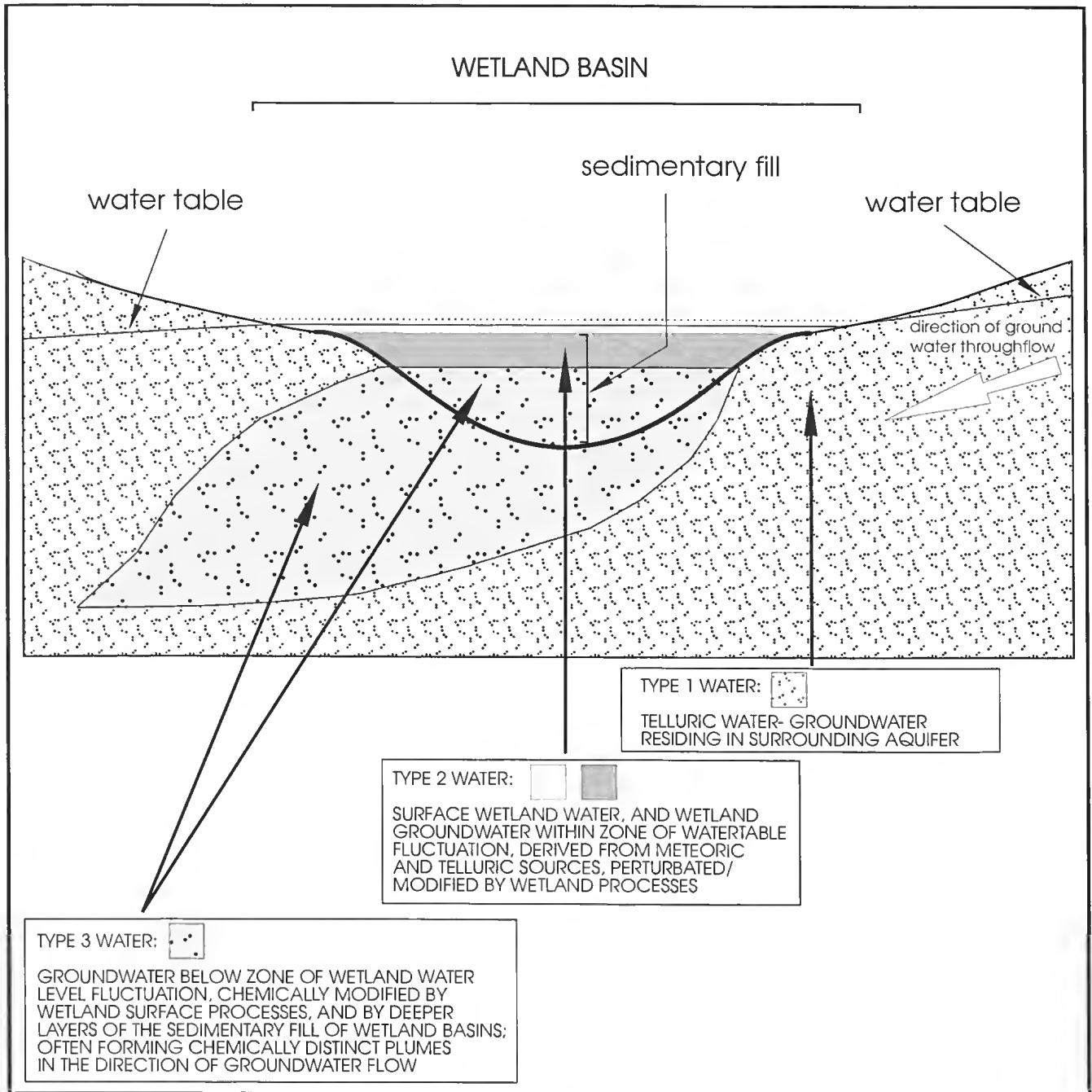
WETLAND BASIN

sedimentary fill

water table

water table

direction of ground water throughflow

TYPE 1 WATER:
TELLURIC WATER- GROUNDWATER RESIDING IN SURROUNDING AQUIFER

TYPE 2 WATER:
SURFACE WETLAND WATER, AND WETLAND GROUNDWATER WITHIN ZONE OF WATERTABLE FLUCTUATION, DERIVED FROM METEORIC AND TELLURIC SOURCES, PERTURBATED/ MODIFIED BY WETLAND PROCESSES

TYPE 3 WATER:
GROUNDWATER BELOW ZONE OF WETLAND WATER LEVEL FLUCTUATION, CHEMICALLY MODIFIED BY WETLAND SURFACE PROCESSES, AND BY DEEPER LAYERS OF THE SEDIMENTARY FILL OF WETLAND BASINS; OFTEN FORMING CHEMICALLY DISTINCT PLUMES IN THE DIRECTION OF GROUNDWATER FLOW

Figure 6. Simplified distribution of hydrochemical patterns of groundwater in and around wetlands.

of the fundamental determinants of the biogenic sediment types generated in wetland basins;

Type 2: surface water and shallow groundwater *within* the wetland; this reflects the chemistry of the source waters (such as direct meteoric input, groundwater throughflow, input of surface water run-off, and artesian/subartesian upwelling), with the overprint of chemical perturbations effected by surface and near-surface processes within the wetlands; and

Type 3: phreatic water residing in wetland sediments and basement materials *under* the wetland surface below the zone of water table fluctuation; this reflects the chemistry of the source waters, descending

plumes of hydrochemically distinct water derived from surface and near-surface of the wetland (and thus the product of biological, chemical, and physical processes at the surface and near-surface of the wetland), and the hydrochemical equilibrium effected on water chemistry by diagenetic processes in the phreatic zone under wetlands; while it may affect the geomorphic and hydrologic evolution of wetlands (*e.g.*, causing dissolution and subsidence in calcareous sediment hosted wetlands, *cf.* C A Semeniuk 2006, or creating relatively impervious layers through diagenetic precipitation of minerals in the subsurface), this water will have little direct effect on the development of sediments on the wetland surface.

The types of water bodies within and around wetlands, their origin, and their generalised hydrochemical signature, are illustrated in Figure 6. This illustration does not address direct meteoric input, which itself, once it enters the wetland, will be modified to a Type 2 water category.

The notion of hydrochemical modification of groundwater by, for example, anoxic wetland sediment, resulting in hydrochemically distinct zones hydrologically up-catchment and down-catchment of wetlands (essentially the water Type 1 *versus* waters Types 2 and 3 of this study) was suggested by Stuyfzand & Moberts (1987) for flow-through lakes in wetlands (dune slacks) in The Netherlands, as a result of using various chemical species such as potassium, nitrate, sulphate, bicarbonate ions, and dissolved organic carbon as tracers to detect hydrochemically distinct plumes. These hydrochemically modified waters also resulted in subsurface sediment modification. For instance, diagenetic zones, with sediment depleted of carbonate in response to the hydrochemically distinct plumes descending down-flow from a wetland, were identified under dune slacks in The Netherlands by Grootjan et al (1996) and Sival & Grootjan (1996).

On the Swan Coastal Plain, phreatic water modified by wetland processes (Type 3 water) has been detected as plumes descending from wetland basins by Allen (1980), Hall (1985), and C A Semeniuk (2006). Similar plumes of wetland-modified water are described in the models presented by Townley et al. (1993) for Jandabup Lake, Thomson Lake, and Nowergup Lake, using Deuterium and Chloride tracers. They identify the outflow zones around lakes as the "release zone". C A Semeniuk (2006) detected diagenetic zones of carbonate dissolution (carbonate depletion) down-flow of a groundwater through-flow system in response to geochemical plumes (equivalent to Type 3 water) under wetlands in the Point Becher area.

Consanguineous wetland setting

A wide range of basin wetland types occurs on the Swan Coastal Plain, varying in size, shape, water characteristics, stratigraphy, vegetation, and maintenance processes (C A Semeniuk 1988; C A Semeniuk et al., 1990): from large linear lakes to small round or irregular seasonally damp wetland basins; from fresh water to hyposaline (brackish) to saline; from surface-water perching to groundwater recharged; their vegetation cover can vary from herbland to forest. These attributes are determined by regional features such as geology, geomorphology, soils, climate and hydrology, and local physical/chemical processes. The variety of wetlands thus formed has been aggregated into natural groupings that have been termed *consanguineous suites* (C A Semeniuk 1988), and these are related to geomorphic setting.

In this paper, the wetlands for stratigraphic study have been drawn from the following consanguineous suites: 1. Becher Suite; 2. Yanchep Suite; 3. Stakehill Suite; 4. Coogee Suite; 5. Balcatta Suite; 6. Bibra Suite; 7. Pinjar Suite; 8 Jandakot Suite; 9 Gnangara Suite; 10. Riverdale Suite; 11. Bennett Brook Suite, and 12. Mungala Suite.

Sediment types

Based on composition and texture, Semeniuk & Semeniuk (2004) recognised ten end-member sediment types in wetlands of the Spearwood Dunes, Bassendean Dunes and Pinjarra Plain on the Swan Coastal Plain, focused only in the central Swan Coastal Plain mainly between Moore River and Mandurah; viz., 1. peat; 2. peat intraclast gravel and sand; 3. calcilutite; 4. carbonate skeletal gravel and sand; 5. carbonate intraclast gravel and sand; 6. diatomite; 7. diatomite intraclast gravel and sand; 8. kaolinitic mud; 9. quartz sand; and 10. quartz silt. However, for completeness of this paper, the full range of the sediments occurring in wetlands of the Quindalup Dunes are included here (C A Semeniuk 1988, 2006). Basins in the Quindalup Dunes contain, as end-member sediments, calcilutite, peat, quartzo-calcareous sand of aeolian origin and, locally, stromatolitic boundstone. Therefore, for purposes of this paper, incorporating the geomorphic settings of Quindalup Dunes, Spearwood Dunes, Bassendean Dunes and Pinjarra Plain, and encompassing the full climatic range of the Swan Coastal Plain from the Bunbury region to Moore River, in total there are 12 end-member wetland sediment types (Table 2).

Mixtures of these end-member sediment types, contributions to peat and diatomite from sponge spicules and phytoliths, and mixtures between the primary sediments and quartz sand (that forms the basement or the margins to the wetland deposits) also occur (Semeniuk & Semeniuk 2004), resulting in spongolitic peat, diatomaceous peat, calcilutaceous peat, spongolitic diatomite, peaty sand, and muddy sand (calcilutaceous muddy sand, diatomaceous muddy sand, and kaolinitic muddy sand), amongst others. The end-member sediment types and the main mixtures between them are described in Table 2 in terms of three sediment suites, viz., fine grained wetland sediments (including both autochthonous and allochthonous sediments), sand/gravel fine grained wetland sediments, and muddy sand wetland sediments.

While Semeniuk & Semeniuk (2004) list and describe a wide range of wetland sediments (see Table 6, *op. cit.*), in places in this paper, the range of fine-grained biogenic wetland sediment types are simplified into three main biogenic sediment groups (the peat-dominated group, the diatom-dominated group, and the calcilutite-dominated group) to convey the three main sources of fine-grained biogenic material contributing to wetland sediments, with the caveat that intergradations between the end-member sediments will occur. The "peat group" contains peat *sensu stricto* (after Semeniuk & Semeniuk 2004), diatomaceous peat, and calcilutaceous peat, the "diatomite group" contains diatomite, organic matter enriched diatomite and calcilutaceous diatomite, and the "calcilutite group" contains organic matter enriched calcilutite and diatomaceous calcilutite.

Geographic distribution of wetland surface sediment types

Surface sediments underlying wetlands vary in their composition east to west across the Swan Coastal Plain according to geologic and geomorphic setting, extant regional to subregional host water chemistry, and biota. The various consanguineous wetland suites of C A Semeniuk (1988) also reside in different geologic and

Table 2

Description of wetland sediments (summarised from Semeniuk & Semeniuk 2004)

Sediment type	Description[1]
Fine grained sediment suite	
peat	black to grey, brown, homogeneous to root-structured to finely laminated, mainly fine-grained organic matter, with root fibres, plant detritus and scattered sand, and freshwater snails (or fragments); some peats with branches, twigs, and logs; often containing diatoms, phytoliths, and sponge spicules; organic matter content > 75%
diatomaceous peat (and spongolitic diatomaceous peat)	peat as above, but with 50–75% organic matter content, and with significant diatom content, and often significant sponge spicule content
calcilutaceous peat	peat as above, but with 50–75% organic matter content, and with significant carbonate mud content
diatomite (and spongolitic diatomite)	light grey, locally dark grey in humus-rich upper layers, homogeneous to root-structured at the surface and laminated at depth; consists of silt-sized to clay-sized diatom tests and particles (and sponge spicules)
organic matter enriched diatomite	grey to brown homogeneous diatomite, as above, but with 25–50% content of organic matter
organic matter enriched calcilutite	grey to brown homogeneous calcilutite, as above, but with 25–50% content of organic matter
calcilutite	cream to pink to grey homogeneous, laminated, burrow-mottled, root-structured, bioturbated, or colour mottled; consists dominantly of clay-sized carbonate particles; mainly calcite, with minor Mg-calcite, aragonite and dolomite, or locally dominantly dolomite; with freshwater snails or fragments
kaolinitic mud[2]	white, orange, dark brown, dark grey to black, homogeneous to root-structured, mostly mud-sized particles with scattered sand; kaolinitic mud is mainly kaolinite, but locally some montmorillonite and sericite; diatoms, sponge spicules and phytoliths are also present
quartz silt	cream to light grey, and structurally homogeneous to root-structured, silt-sized and some clay-sized silica particles, with scattered quartz sand; diatoms, sponge spicules and phytoliths are also present
Sand/gravel sediment suite	
peat intraclast gravel and sand	black to grey, breccioid often termed "peat breccia" in this paper to conglomeratic, grading to sand-sized clasts of peat, or alternating layers of breccia, conglomerate, and sand-sized fragments of indurated peat; may be texturally layered, and root-structured
carbonate skeletal gravel and sand	cream to grey, homogeneous to layered; very coarse to medium sand; consists of whole and fragmented skeletons of molluscs
carbonate intraclast gravel and sand	cream to grey, structurally homogeneous to layered, with local vesicular to fenestral structures; consists of medium, coarse to very coarse intraclasts of calcilutite or cemented aggregates of carbonate sand
diatomite intraclast gravel and sand	light grey, rounded fine gravel- to sand-sized clasts of diatomite
quartz sand[3]	white, light grey to dark grey sand, homogeneous to bioturbated to root-structured; locally with wispy lamination, or with vesicular structure; quartz, with minor feldspar
quartzo-calcareous sand	white, light grey to dark grey sand, homogeneous to bioturbated to root-structured; consists of quartz, carbonate grains
Muddy sand sediment suite	
peaty sand	quartz sand as above, but with fine-grained interstitial material with > 75% organic matter
calcilutaceous muddy sand	quartz sand as above, but with interstitial carbonate mud
diatomaceous muddy sand	quartz sand as above, but with interstitial diatom mud
kaolinitic muddy sand	quartz sand as above, but with interstitial mud-sized phyllosilicate mineral particles and quartz silt

[1.] there is also a range of diagenetic products that form in wetland sediments (Semeniuk & Semeniuk 2004); these include carbonate cements and nodules, micro-etched surfaces (indicating dissolution) on biogenic silica, the bio-mediated precipitates of FeS_2 as framboidal pyrite, the sulphides of heavy metals and metalloids; these diagenetic products are not described in detail here.

[2.] the sediments formed as mixtures between kaolinitic mud and the biogenic mud of peat, diatomite, and calcilutite (Semeniuk & Semeniuk 2004) are not common sediments (the most common of this suite being organic matter-enriched kaolinitic mud, diatomaceous kaolinitic mud, and organic matter-enriched diatomaceous kaolinitic mud).

[3.] quartz sand here is not the parent basement sand, but extrabasinal, transported *into* the wetland basin.

geomorphic settings, each often with its own diagnostic basement materials such as quartzo-calcareous sand, limestone, yellow quartz sand, white quartz sand, and fluvial terrigenous sediments. As a consequence, sediment types filling wetland basins, or forming along the margins of the basins reflect these geomorphic and consanguineous settings: firstly, because of the hydrochemical setting, and secondly because of the direct sediment contribution from the surrounding uplands (*e.g.*, quartz sand shed by sheet wash or wave reworking into wetland margins in the Bassendean Dunes, quartzo-calcareous sand shed by sheet wash, wave reworking, or aeolian agency into wetland margins in the Quindalup Dunes, or fluvial clay delivered by rivers and alluvial fans into basins on the Pinjarra Plain).

Wetland hydrochemistry and hence sediment types reflect regional to local hydrochemistry, as determined by source of water (local groundwater, subregional groundwater, meteoric water, and surface water inflow), or by intrabasinal perturbations. For example (as noted above), groundwaters residing in quartz-sand-rich terrain (such as the Bassendean Dunes) will be Ca-and-HCO_3 depauperate, and groundwaters residing in limestone terrain (such as the Spearwood Dunes) and calcareous coastal dunes (such as the Quindalup Dunes) will be locally Ca-and-HCO_3 enriched (Table 1).

Wetland hydrology and hydrochemistry underpin biotic responses and hence will influence the type of biogenic sediment that may accumulate. There will be a variety of biogenic sedimentary fills in any east-west transect in relation to hydrochemistry and geomorphic setting. Sediment type may be the direct product of biogenic activity, producing particles that accumulate *in situ* or are transported to other sites in the basin: vegetation contributes to the development of fibrous and massive peat, and development of organic matter enriched calcilutite and diatomite; diatoms contribute to the development of diatomite, diatomaceous peat and diatomaceous calcilutite; and charophytes and calcareous invertebrate fauna contribute to the development of calcilutite, calcilutaceous peat and calcilutaceous diatomite.

There also will be a pattern in the distribution of wetland surface biogenic sediment types geographically from south to north in relation to climate. For instance, climate affects the geographic distribution, abundance, and productivity of plant forms and species. As a consequence, for example, similar wetland basins residing in the Bassendean Dunes may be peat dominated in the southern wetter parts of the Swan Coastal Plain, and diatomite dominated in the drier northern parts of the Plain. The occurrence and productivity of plant forms also will vary across a wetland basin, and hence regulate the type of sediment filling different parts of the basin.

A description of surface sediments of wetland basins across the Swan Coastal Plain, from the Pinjarra Plain to the Quindalup Dunes in relation to their geological and hydrochemical setting is provided below.

Wetland basins on the Pinjarra Plain along the eastern Swan Coastal Plain range from lakes to sumplands to damplands, and are associated with terrigenous sediments of river courses. The sumplands and damplands tend to be shallow depressions underlain by

extrabasinal sediments, such as sand, kaolinite-dominated mud and muddy sand, reflecting sediment delivery and sedimentation by fluvial processes. Basin fills within the Pinjarra Plain are kaolinitic mud, muddy sand, sand, or peat. Diatoms and phytoliths contribute subdominant to minor fine-grained biogenic silica to such sediments as fine grained interstitial material (Semeniuk & Semeniuk 2004).

Within the Bassendean Dunes, the basins reside in a terrain of quartz sand, and the wetlands are lakes, sumplands, and damplands. The waters tend to be cation-poor, tannin-rich, and acidic (to alkaline). The surface sediments underlying the wetlands are intrabasinal peat, diatomaceous peat, and diatomite, and extrabasinal kaolinitic mud, and quartz sand. Within the Spearwood Dunes, the basins reside in a terrain of quartz sand and/or limestone, and the wetlands are lakes and sumplands. The waters are cation-enriched and range from tannin-rich to tannin-poor, and alkaline (to acidic). The sediment fills are intrabasinal peat, diatomaceous peat, or calcilutite, and extrabasinal quartz sand. Surface sediments underlying wetlands are peat, diatomaceous peat, calcilutite, organic matter enriched calcilutite, and locally, quartz sand. Within the Quindalup Dunes, the basins reside in a terrain of quartzo-calcareous sand and the wetlands are lakes, sumplands, and damplands. The groundwaters are cation-enriched, and range from tannin-rich to tannin-poor, and alkaline (to acidic). The sedimentary fill is intrabasinal calcilutite, and some peat, and extrabasinal quartzo-calcareous sand.

The occurrence of the surface wetland sediments with respect to the wetlands studied on the Swan Coastal Plain is presented in Figure 7. For purposes of this illustration, the wide range of wetland sediment types are simplified into the three fine-grained biogenic groups (*viz.*, peat, diatomite, calcilutite), and two types of terrigenous sediment (*viz.*, kaolinite mud, and extrabasinal sand). In many wetlands, there are strong internal facies changes within the central zone, so that two or more sediments are used to characterise that particular wetland. Facies changes at the margin (periphery) of wetlands (such as organic matter enrichment, or muddy sand facies) are ignored in this presentation. In a number of wetlands, typical of those in the Bassendean Dunes, there is no wetland sediment but rather waterlogged basement sand (these are noted as "sand" on the map). Figure 7 does not address lithologies that may be present at depth (*i.e.*, if the surface sediment is calcilutite, and the subsurface sediment at > 30 cm depth is diatomite, the extant surface sediment is noted as calcilutite). In general therefore, each sampling site is noted by a single sediment type. However, where two sediment types are co-dominant in a basin, both are included at that site on the map. For muddy sands, the mud component only is noted on the map (*e.g.*, calcilutaceous muddy quartz sand is noted as calcilutite, as the generation of carbonate mud is considered to be the critical factor in showing the distribution of sediments in relation to geomorphic and geographic setting even if that carbonate mud is admixed with parent quartz sand). However, using only the mud component of muddy sands in the map of Fig. 7 was not a major issue in this study as most wetland basins encountered usually were clearly dominated by fine-grained wetland sediment.
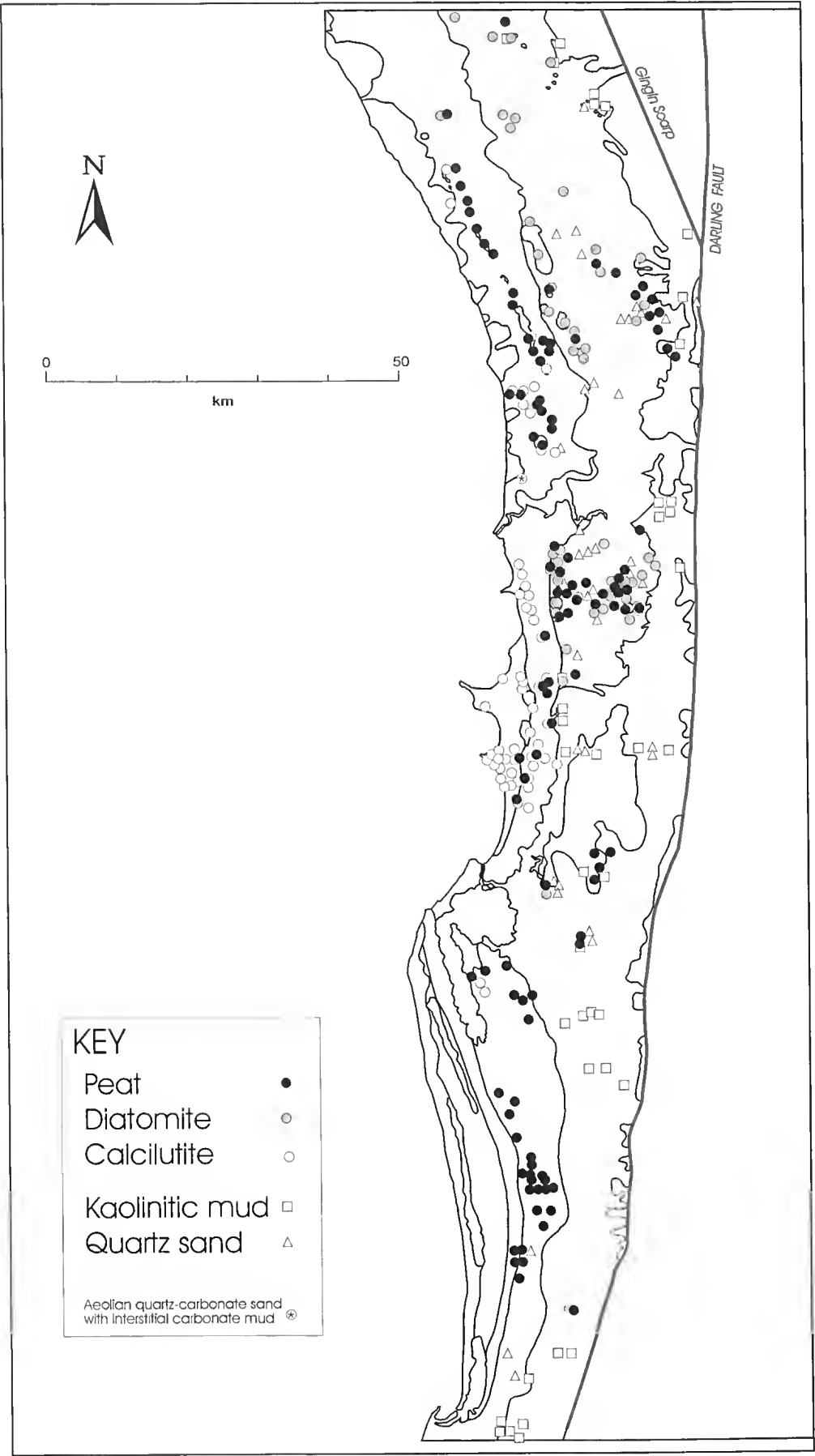
Figure 7. Sediment types at the sampling sites, showing the dominant sediment in the wetland. The outline of the geomorphic units in Figure 5 is shown unlabelled in this illustration to indicate the relationship of sediment type to geomorphic setting, and the reader will need to refer to Figure 5 to determine the geomorphic setting of a particular sampling site.

Table 3

Dominant surface sediment types in key consanguineous wetland suites, central Swan Coastal Plain in relation to geomorphic setting and lithology through which source (telluric) groundwater has been derived.

Geomorphic setting	Consanguineous wetland suite	Lithologic context for telluric water	Dominant surface sediment type[1,2]
Quindalup Dunes	Becher	calcareous sand	calcilutite, and organic matter enriched calcilutite
Quindalup Dunes	Peelhurst	calcareous sand	calcilutite, organic matter enriched calcilutite, and quartzo-calcareous sand
Quindalup Dunes	Cooloongup	calcareous sand and limestone	calcilutite, intraclast sand and gravel, stromatolitic boundstone
Spearwood Dunes	Yanchep	limestone and quartz sand	calcilutite, peat, diatomaceous peat
Spearwood Dunes	Stakehill	limestone and quartz sand	calcilutite, peat
Spearwood Dunes	Coogee	limestone and quartz sand	calcilutite
Spearwood Dunes	Balcatta	quartz sand and limestone	peat, calcilutite
Spearwood/Bassendean Dunes contact	Bibra	quartz sand	diatomite, (and organic matter enriched diatomite)
Spearwood/Bassendean Dunes contact	Pinjar	quartz sand	diatomite
Bassendean Dunes	Gnangara	quartz sand	diatomite, peat
Bassendean Dunes	Jandakot	quartz sand	diatomite, peat
Bassendean Dunes	Riverdale	quartz sand	peat, diatomaceous peat
Bassendean Dunes/ Pinjarra Plain contact	Bennett Brook	quartz sand, muddy sand	kaolinitic mud, muddy sand, sand, peat
Pinjarra Plain	Mungala	quartz sand, muddy sand	kaolinitic mud, muddy sand, sand

[1] lithologic terms for the sediments, and the range of sediment types occurring within a consanguineous suite may differ from those in C A Semeniuk (1988), firstly, because the wetland sediment terms have been refined (following Semeniuk & Semeniuk 2004), and secondly, because more detailed work has been carried out in the wetland suites.

[2] the variation in sediments within a suite can occur as a result of sediments varying from wetland to wetland within a suite, and also can reflect the variation of sediments across a given basin and down the stratigraphic profile.

A summary of the east-west pattern of sedimentary fills in wetlands related to consanguineous setting is presented in Table 3.

Intrabasin variation in surface sediment types

Surface sediments can vary laterally within a given basin, i.e., there can be facies variation within basins. The most prominent and consistent variation is that of sediments of the central part of a basin grading into the sediments along the margin of a basin. Peat, diatomite, calcilutite, or kaolinitic mud of the central basin grade into peaty sand, diatomaceous muddy sand, calcilutaceous muddy sand, or kaolinitic muddy sand, respectively along wetland margins. Peat, diatomite, calcilutite, or kaolinitic mud of the central basin also may adjoin aprons of quartz sand, peat intraclast sand/gravel, diatomite intraclast sand/gravel, carbonate intraclast sand/gravel, and shell sand/gravel. Facies changes also are noted where diatomite or calcilutite of non-vegetated central parts of a basin grade into a zone of peripheral vegetation (with concomitant increased production of macrophytes and accumulation of organic matter and sponge spicules); this results in a peripheral zone of sediment composed of organic matter enriched diatomite, spongolitic organic matter enriched diatomite, organic matter enriched calcilutite, spongolitic organic matter enriched calcilutite, peat, or spongolitic peat. Facies changes also occur *within* the central basin: for example, diatomite, calcilutite or peat may be laterally facies equivalents of each other. Such intrabasin lateral facies variation often reflects various types of water regimes within a basin, or local microscale topographic variation, or where vegetation type strongly influences sediment type, the mottling and heterogeneity of vegetation (*cf.* C A Semeniuk *et al.* 1990)

Wetland stratigraphy

Wetland stratigraphy is described in terms of the main sedimentary sequence filling the central basin, and its variation, and in terms of its basal and marginal contacts. The intrabasinal depositional categories of Semeniuk & Semeniuk (2004), *viz.*, central facies, basal facies, and marginal facies are used here. Note should be made that while Semeniuk & Semeniuk (2004) emphasised the Pleistocene age of the basement that formed the foundation to wetland basins in the Spearwood Dunes, Bassendean Dunes and Pinjarra Plain systems, wetland basins within the Quindalup Dunes reside in a terrain of Holocene age (C A Semeniuk 2006). Hence, as noted earlier, the basement to wetland basins can be Pleistocene sediment, or Holocene sediment. The variation in wetland stratigraphy is shown in Figures 8, 9, 10 and 11.

Figure 8 shows a range of cores, illustrating lithology

and structures, down-profile variation in lithology, contact types, across-basin facies changes, and some specific features such as burrow structures, charcoal horizons, and breccia (*i.e.*, intraclast) units. The details of these cores shown in Figure 8 also supplement the stratigraphic sections shown in Figures 9, 10 and 11 by providing lithologic detail for some selected stratigraphic sequences. The core from Lake Cooloongup illustrates sedimentary structures, bioturbated contacts, the capping of a calcilutite sequence by peat, and the gradational relationship between calcilutite and underlying sand. The cores from Lake Gwelup show the lateral change in a stratigraphic contact between (shelly) organic matter enriched calcilutite and underlying calcilutite; it grades from sharp contact to burrowed contact over 20 m. The cores from Lake Manning show burrow-punctured laminated calcilutite and colour variation in the laminated calcilutite from the central basin, decimetre-interlayered organic matter enriched calcilutite and grey calcilutite from the marginal facies, and the muddy sand contact between calcilutite and underlying sand in the basal facies under the central basin. The core from Lake Coogee shows grey, laminated calcilutite overlying, with sharp contact, a layered to burrow-structured shelly and intraclastic calcilutite. The core from Beenyup Swamp shows an upper part of fibrous peat interlayered on a decimetre scale with diatomaceous peat, and a lower (deeper) section composed of root-structured, bioturbated, fibrous peat with charcoal horizons. The cores from Lake Mealup show stratigraphic variation over 20 m: laminated peat is overlain by brecciated peat in one core, and by root-structured, bioturbated, fibrous peat and then brecciated peat in another core. The surface cores of peat breccia from Beenyup Swamp, Lake Mealup, and Melaleuca Park show the relationship of peat breccia to an underlying microbrecciated peat, crudely laminated peat, and root-structured, bioturbated, fibrous peat, respectively.

Figure 9 shows a range of lithological sequences to illustrate the variety of stratal types in the wetlands, and a variety of sedimentary fill thickness, focusing on the stratigraphy of groups of sections exhibiting terrigenous sediment dominated sequences, diatomite-dominated sequences, peat-dominated sequences, calcilutite-dominated sequences, peat sand dominated sequences, and mixed (lithologic) sequences. The cores of biogenically derived sediment (diatomites, peats, and calcilutites) generally show the gradational muddy sand transitional zone between fine grained biogenic sediment and the underlying basement sand, however, one core (Site 6) at Casuarina Swamp shows a relatively thick sequence of diatomaceous muddy sand. The cores illustrating mixed lithologic sequences show quite variable interlayering of lithology from site to site, with no regionally consistent pattern.

Figures 10 and 11 illustrate cross-basin stratigraphy and stratigraphic relationships for a variety of small to large wetlands that are peat-dominated, diatomite-dominated, calcilutite-dominated, those with mixed lithologic sequence, and those filled with terrigenous sediment. These cross sections, to be described later in the paper, illustrate variation in ancestral basin profile, asymmetry in wetland basin fill, variation in thickness of the sedimentary fill, asymmetry in stratigraphy, and various types of basal and lateral facies relationships.

The central facies – the main sedimentary fill

The types of sediments filling wetlands may form varying sequences within the main body of the wetland, *i.e.*, the central facies of the wetland sedimentary fill. The stratigraphy may be composed entirely of a single fine-grained end-member sediment type (*e.g.*, diatomite, or peat), homogeneous mixtures of the end-member sediment types (*e.g.*, diatomaceous peat, or organic matter enriched calcilutite), interlayered sequences of the sediments, texture-mottled mixtures of the end-member sediments, or interlayered sequences of lithologically similar but structurally distinct layers. Figure 9 illustrates a selection of stratigraphic profiles, as single cores, from peat-dominated wetlands, diatomite-dominated wetlands, calcilutite-dominated wetlands, terrigenous sediment dominated filled wetlands, and those with mixed stratigraphy.

Sediment fill in wetland basins, as measured in the basin centre, varies in thickness from 0.1 m to 7 m. Most wetland sedimentary fill in basins on the Swan Coastal
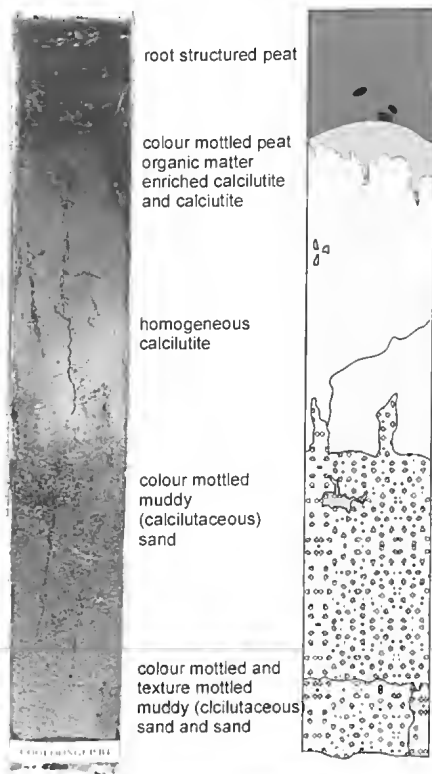
Table 4

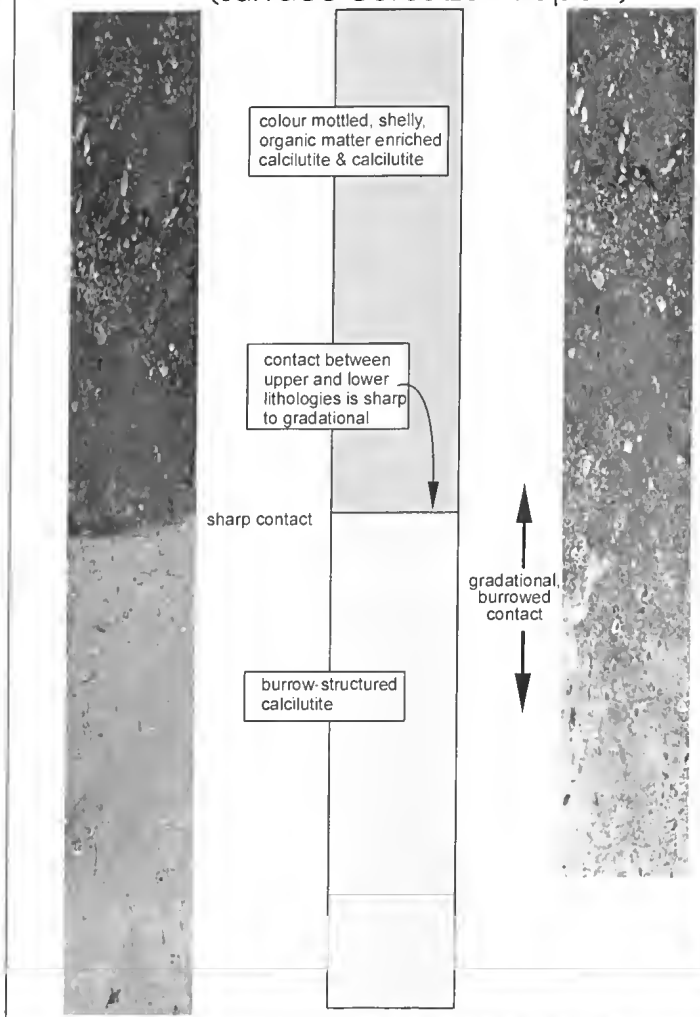Standard stratigraphic sequences within Swan Coastal Plain wetlands

Style of stratigraphy	Type location
thick peat (> 2 m)	Karrinyup Road Swamp
thick peat and diatomaceous peat (> 2 m)	Waluburnup Swamp
medium thickness peat and diatomaceous peat (1–2 m)	Stakehill Swamp
thin peat and diatomaceous peat (< 1 m)	Melaleuca Park Swamp
thick calcilutite (> 2 m)	Lake Manning
thin calcilutite (< 1 m)	Cud Swamp
thin calcilutaceous muddy sand (< 0.1 m)	1N Becher wetlands
thin peat on thin calcilutite	Wawa Swamp
thin diatomite on thick calcilutite	Lake Forrestdale
alternating peat and calcilutite	Leda Swamp
peat, calcilutite, quartz sand	Little Carine Swamp
peat, kaolinitic mud, quartz sand	Ellenbrook Swamp
thick diatomite (> 2m)	North Lake
thin diatomite and diatomaceous sand	Lake Pinjar
diatomite, kaolinitic mud, quartz sand	Coonabidgee Swamp

Figure 8. Selection of single-cores to illustrate the range of structures present in the sediments. Core relate to selected sites and depths of cores and transects shown in the illustrations of Figures 9 and 10.
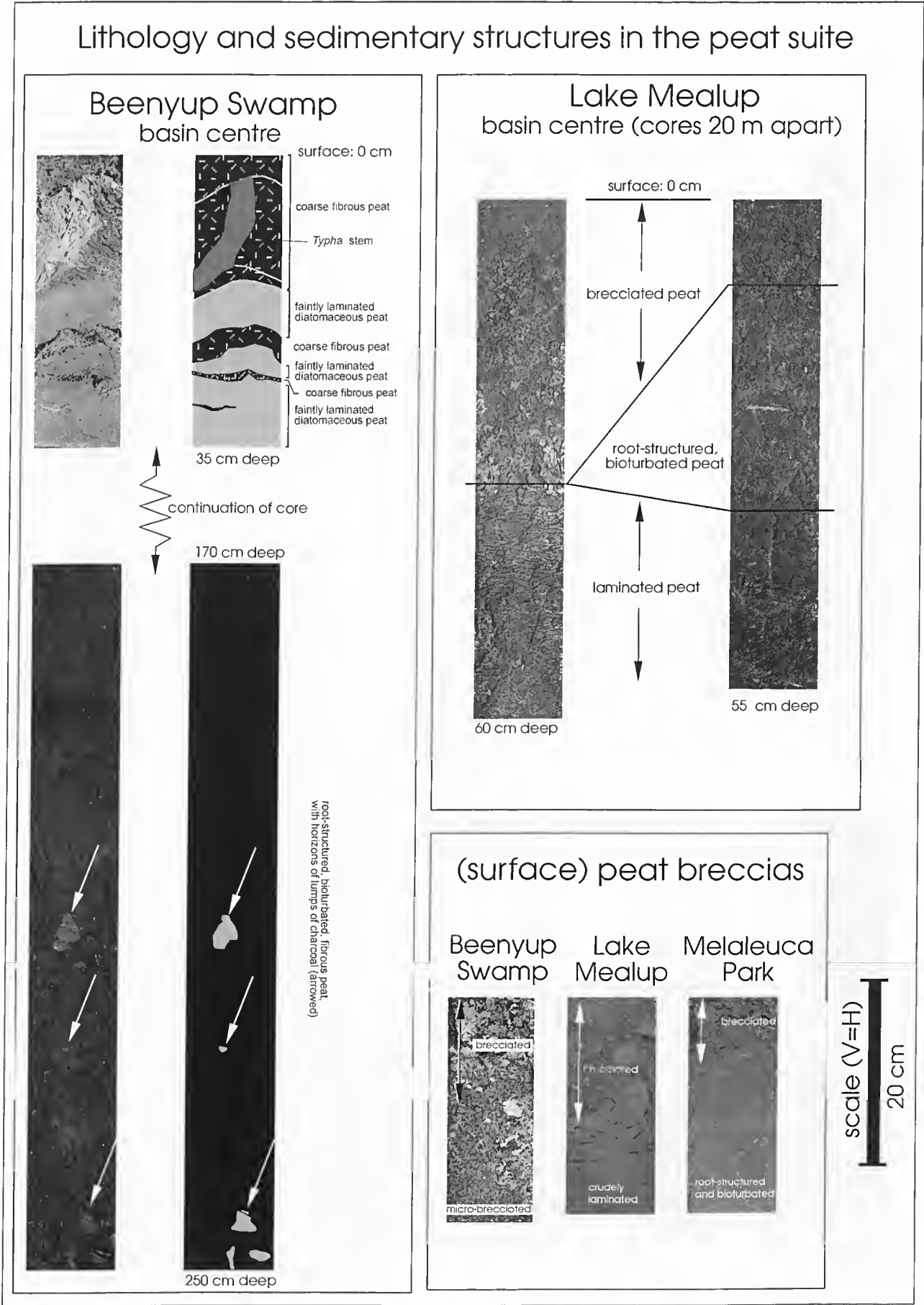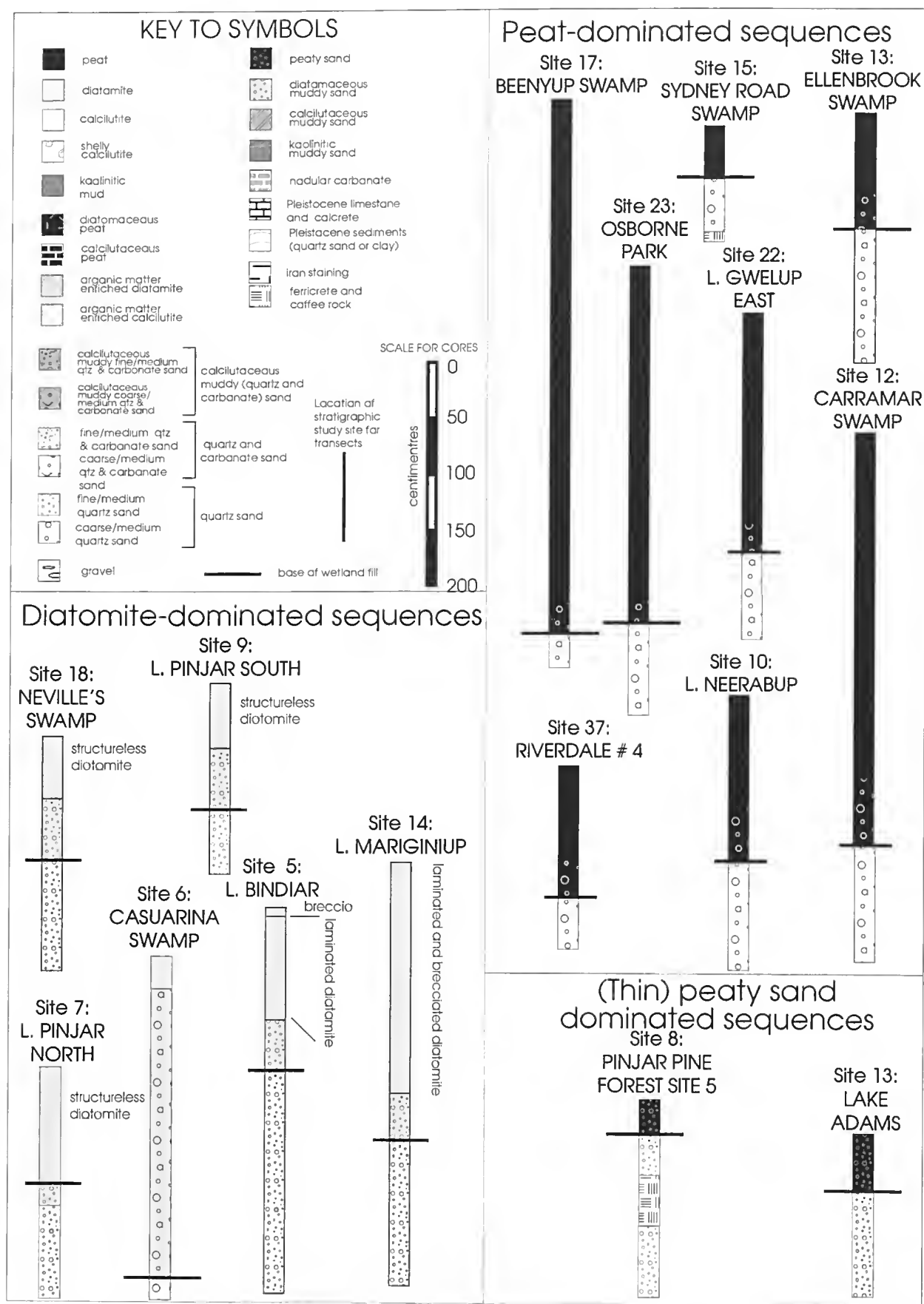
Figure 8 (cont.)

Figure 9. Selection of single-core stratigraphic profiles from various wetlands from sites 1–37 of Figure 4 showing sequences that are peat-dominated, diatomite-dominated, calcilutite-dominated, terrigenous sediment dominated, and of mixed lithology. Location of cores is shown in Figure 4. The lithologies of quartz and carbonate sand, and their muddy sand equivalents, are simplified from C A Semeniuk (2006), and apply only to the wetlands in the Becher Suite. Key to lithologies in this Figure also applies to the Transects shown in Figures 10 and 11.
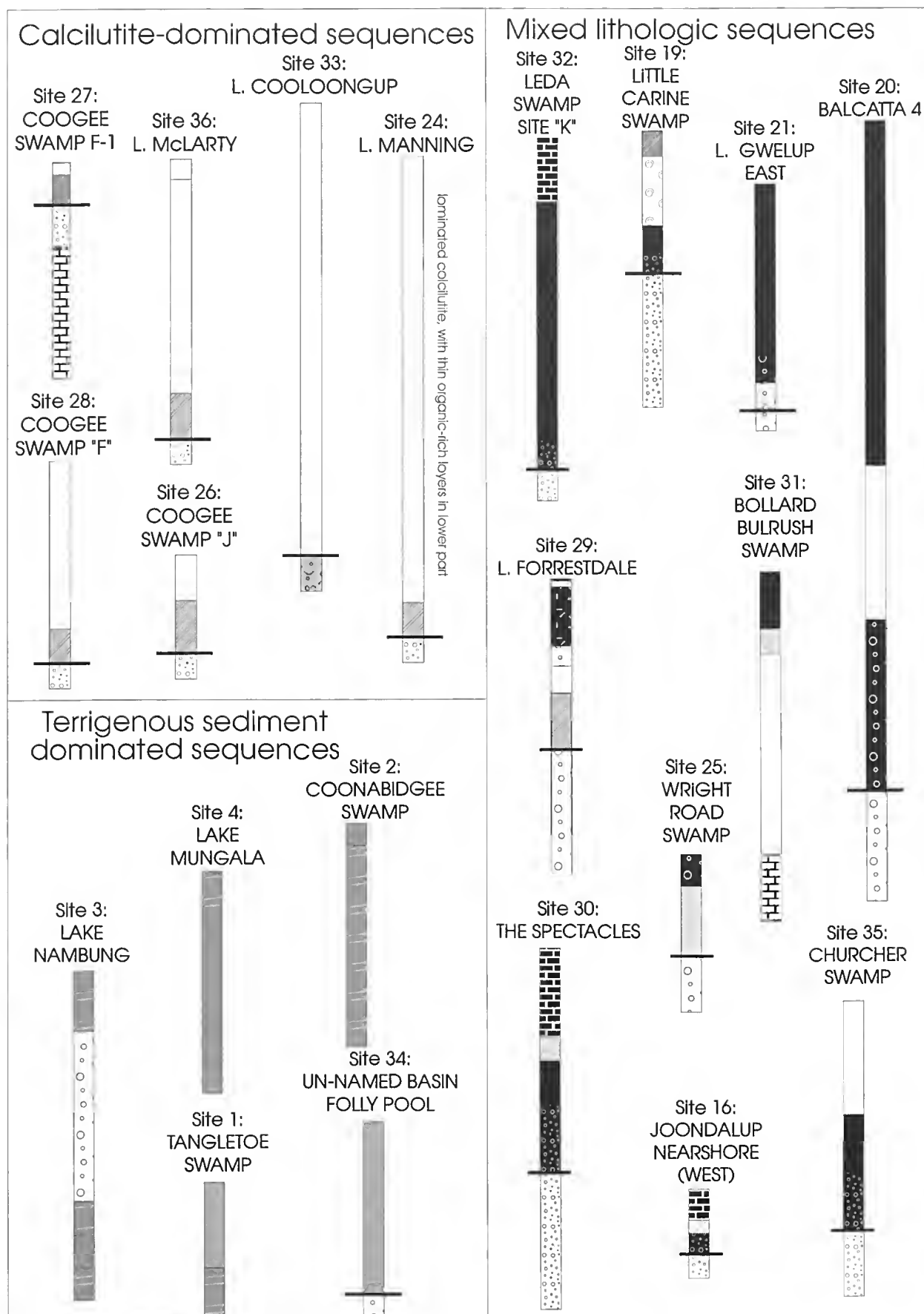
Figure 9 (cont.)

Plain is 1–1.5m thick. Peats range from 0.3 m to 7 m; calcilutites range from 0.2 m to over 4 m; diatomites range from 0.1–3 m generally; and kaolinitic mud deposits range from 0.1–0.2 m.

Fifteen standard sequences are recognised in the sedimentary fill of wetlands in the Quindalup Dunes, Spearwood Dunes, Bassendean Dunes, and Pinjarra Plain. These standard sequences, with some variation in thickness of units therein, recur throughout the wetlands of the Swan Coastal Plain. The standard sequences and type locations (where best developed) are listed in Table 4.

Locally, in some wetlands, there is lateral stratigraphic variation in the interior of the wetland sedimentary fill, *i.e.*, intrabasin lateral variation of stratigraphy of the central facies that reflect, originally, isochronous intrabasin lithologic variation rather than diachronous vertically accreting lithologies. Some of the isochronous lateral variations involve changes in lithology from peat to diatomite, or fibrous peat to laminated peat, or peat to calcilutite. Where directly observable (because of engineering excavations and dewatering), these stratigraphic changes appear as lithologically distinct lenses with sharp to gradational boundaries.

Contact of the main sedimentary fill to the basement

The base of wetland fills tends to be gradational into the underlying Pleistocene or Holocene materials. Peat, diatomite, or calcilutite overlying basement quartz sand have a gradational zone of infiltrated or bioturbated wetland sediment resulting in peaty sand, diatomaceous sand and calcilutaceous sand, respectively (Figures 9, 10, and 11).

The marginal facies

The marginal facies of the wetland sedimentary fills reflect two processes: 1. changes in lithology in wetland sediments in margin situations; and 2. the interaction of wetland sediments with the basement materials within which the wetland resides. As a result, two types of marginal facies are recognised: the inner marginal facies derived directly from the main sedimentary fill of the wetland, and an outer marginal facies derived from the mixing of wetland sediment with basement material. In many instances, the inner marginal facies is mixed with basement material to form a plethora of sediment types in the outer marginal facies.

The development of the inner marginal facies results from the fact that wetland margins are the environments, or facies, that experience extremes of physical environmental conditions. Additionally, they may support specific plant and faunal assemblages, or experience specific hydrochemical conditions (*e.g.*, such as Ca-enriched seepage from the upland into the wetland). Wetland margins, for instance, axiomatically, are the first parts of a wetland to dry out with the falling of water levels during the annual hydrologic cycle, and hence undergo desiccation, and hydrochemical changes (see below). They are the zones where fires may be concentrated, or where fires are most frequent, and hence may accumulate the products of pyrogenesis. Where there are seasonal hydrochemical changes, wetland margins may develop crusts, and other diagenetic products. If there is a peripheral vegetation zone, wetland margins may preferentially accumulate plant material and hence become enriched with organic matter. If there is a peripheral vegetation zone of sedges, they may preferentially accumulate concentrations of phytoliths. If there is a peripheral vegetation zone of trees or sedges, they may preferentially accumulate concentrations of sponge spicules. The shallow water margins are zones of foraging, burrowing and other faunal activities, resulting in bioturbation of sediments. If there is shoreward transport of sediment under wave action, wetland margins may accumulate shore-distinctive facies, such as shell ribbons, sand ribbons, or beachridges. Desiccation of peat, diatomite, and calcilutite may generate sheets of intraclast gravel and sand, which, by wave action, may accumulate as shore-parallel littoral ribbons, or as nearshore wave-oriented isolated ripples and bars.

The range of sediments that accumulate in the marginal facies in modern environments are listed according to their primary central basin lithology, *i.e.*, peat, diatomite, calcilutite (Table 5). It is stressed here that these marginal facies are not the product of wetland sediments interfacing with the basement materials but rather the facies changes that occur as wetland sediments are subjected to physical, chemical and biological processes associated with environmental conditions of shallow water, shoreline seepages, peripheral wetland biotic activities by fauna and flora, and drying out.

Wetland sediments also must interact with the basement material along their margins, producing a range of sediments types. The margins of the wetland

Table 5

Lithologies in the inner marginal facies derived from the three main fine-grained biogenic sediments

| Primary central basin lithology	Inner marginal facies (in lateral contact with central facies)
peat	fibrous and root-structured peat, phytolith-bearing peat, spongolitic peat, peat intraclast gravel and sand (ie peat breccia and microbreccia) sandy peat
diatomite	structureless diatomite, root-structured diatomite, bioturbated diatomite, organic matter enriched diatomite, phytolith-bearing diatomite, spongolitic diatomite, diatomite intraclast gravel and sand, diatomaceous muddy quartz sand, sandy diatomite, sandy organic matter enriched diatomite
calcilutite	skeletal gravel and sand, organic matter enriched calcilutite, spongolitic calcilutite, root-structured calcilutite, bioturbated calcilutite, carbonate intraclast gravel and sand, sandy calcilutite, sandy organic matter enriched calcilutite
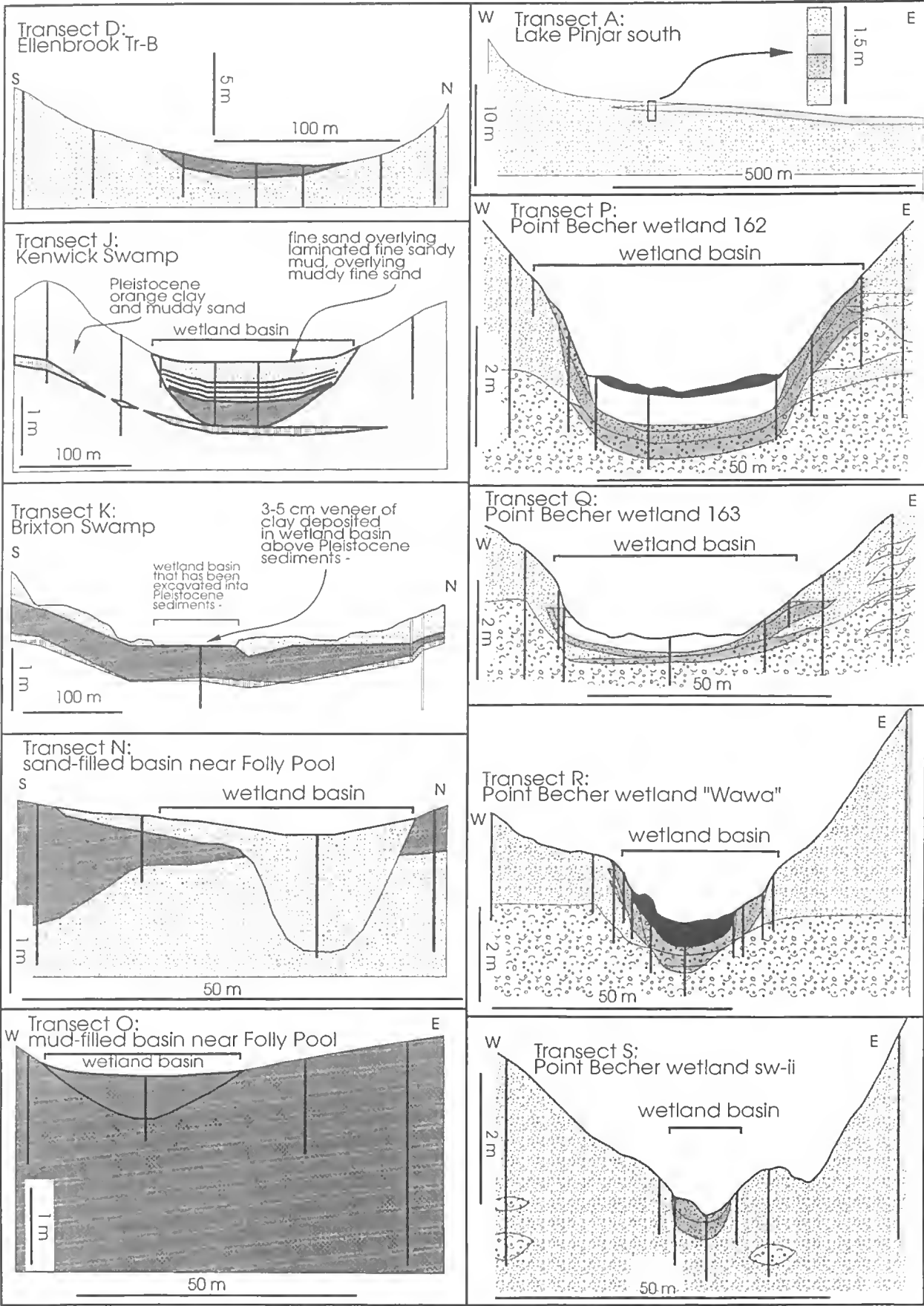
Figure 10. Stratigraphy of selected wetland basins from a number of locations, Transects A to V (excluding I), showing cross-basin variation in terms of lithological homogeneity or heterogeneity of sedimentary fill, and details of the central facies, and marginal and basal relationships. Location of cores is shown in Figure 4. Description of the transects is presented in the text. The cross sections from Point Becher (Transects P, Q, R and S) are modified from C A Semeniuk (2006). The extent of the wetland basin indicated on each transect provides indication generally of where high water levels reach.
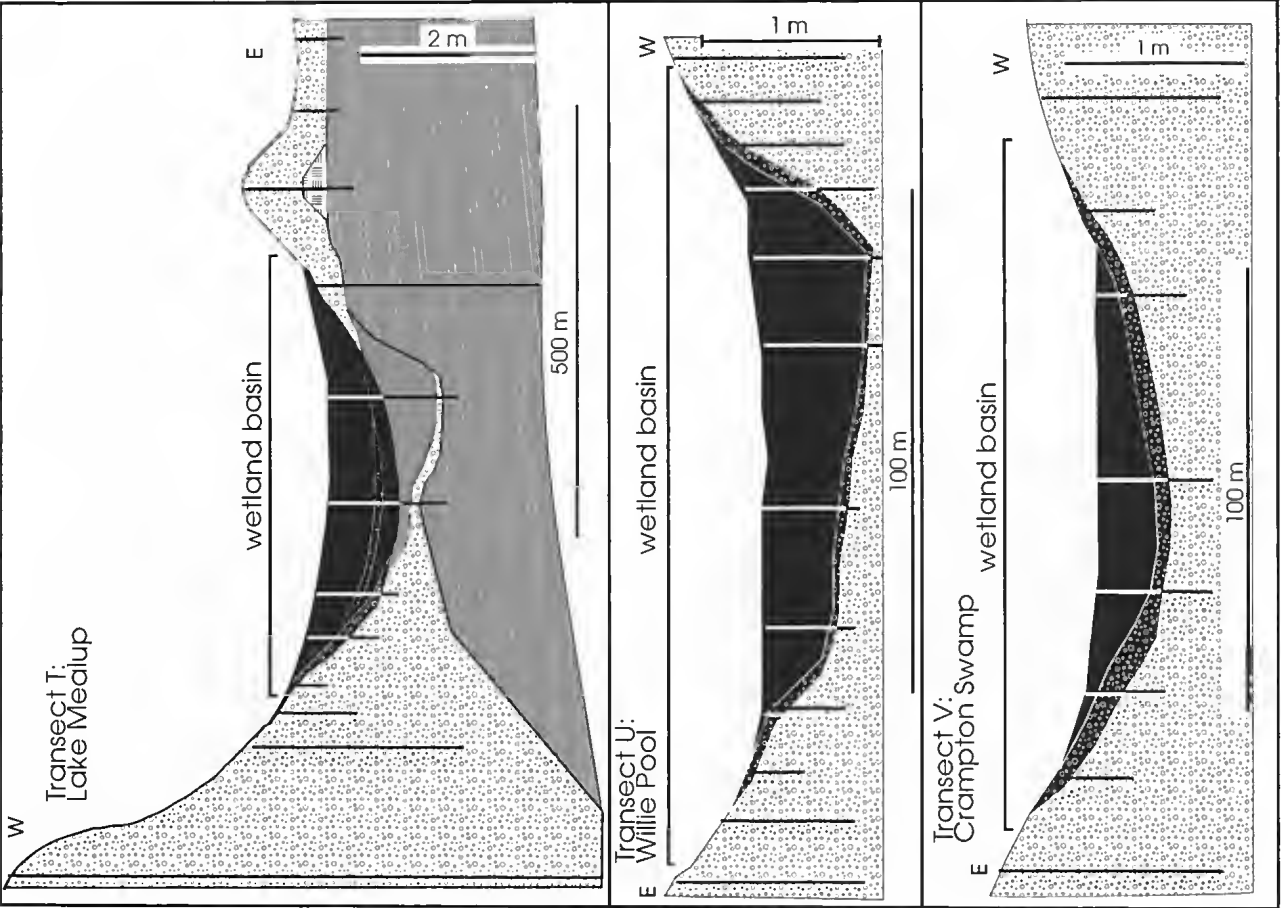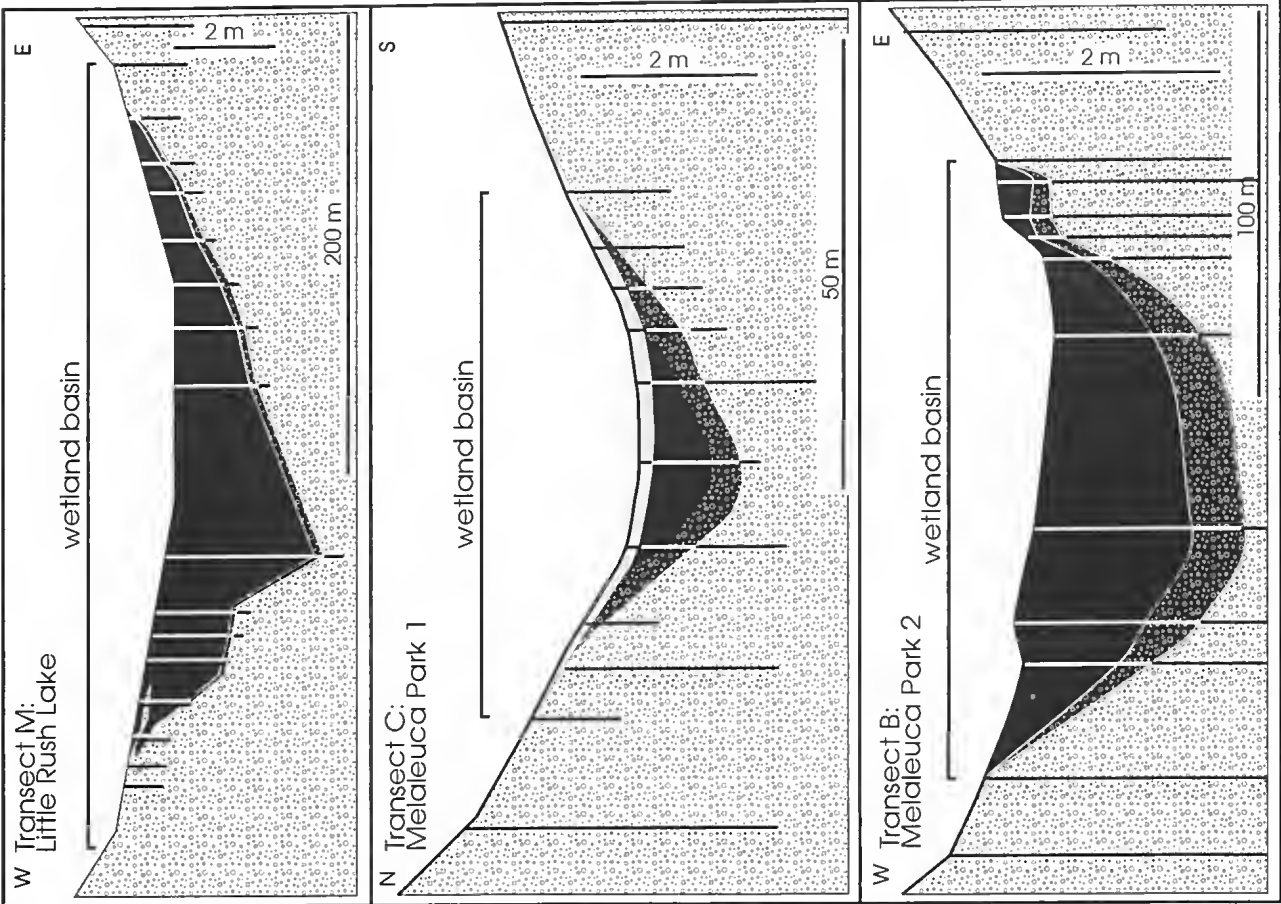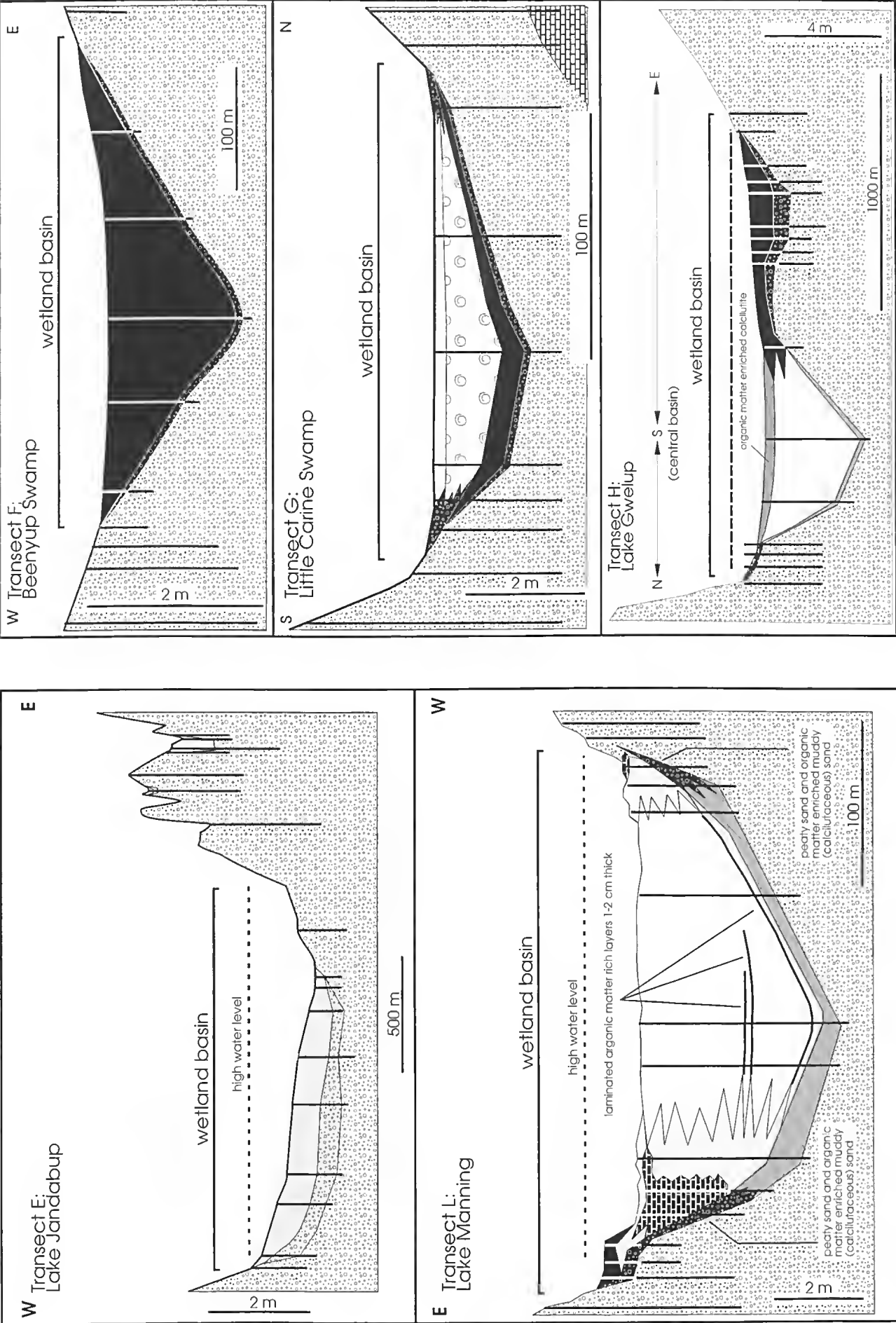
Figure 10 (cont.)

Figure 10 (cont.)

Table 6

Lithologies in the outer marginal facies derived from the three main fine-grained biogenic sediments

Primary central basin lithology	Outer marginal facies (in lateral contact with basement)
peat	peaty quartz sand, sandy peat
diatomite	diatomaceous muddy quartz sand, sandy diatomite, sandy organic matter enriched diatomite
calcilutite	calcilutaceous muddy quartz sand, calcilutaceous muddy quartzo-calcareous sand, sandy calcilutite, sandy organic matter enriched calcilutite

fills may have an interfingering relationship with reworked deposits of the surrounding Pleistocene or Holocene sediments (Figures 10 and 11), or may have a gradational contact. That is, peat, diatomite, or calcilutite of central wetland basins may grade laterally via peaty sand, diatomaceous muddy sand, and calcilutaceous muddy sand into the quartz sand and quartzo-calcareous sand of the basement margins, or wedges, sheets and tongues of quartz sand or quartzo-calcareous sand reworked from the margins may penetrate to a limited distance into the layers of the wetland fills. Where the sand bordering the margin of the wetland is reworked into shore-perpendicular to shore-oblique sand waves, the extension of the sand into the wetland sediments appears as a series of sand tongues or if bioturbated, muddy sand tongues penetrating into the wetland sediments. Where the basement materials directly interface with inner marginal facies, a complex mixture of sediment types are produced. Table 6 lists the range of marginal facies sediments produced in simple situations where end-member sediments of peat, diatomite and calcilutite directly interface with the basement materials.

Summary of intrabasin facies relations

For many wetland basins, the three facies, *i.e.*, central, basal, and marginal, often can be recognised. Table 7 summarises the facies types encountered in cross-basin stratigraphy for each of the main wetland biogenic sediment types with some typical examples. Specific intrabasin relations of central facies to the wetland margins and to the basal facies are illustrated in Figure 12.

In terrigenous sediment settings, where there is kaolinitic mud accumulating in the central basin, the basal facies is muddy sand, and the marginal facies is muddy sand and phytolithic muddy sand, as exemplified by Tangletoe Swamp and Lake Mungala.

Description of specific transects

A range of transects through wetland basins across and along the length of the Swan Coastal Plain are presented in Figures 10 and 11. These have been selected to illustrate a variety of basin settings for the sedimentary fill, a variety of vertical and lateral stratigraphic relationships, the symmetry or asymmetry of the ancestral wetland basin, and hence the symmetry/asymmetry of the wetland sedimentary lithotope, the variety of internally homogeneous or heterogeneous stratigraphic sequences, and the symmetry or asymmetry of facies across the basin. Annotated photographs of selected cores from specific depths and specific facies from these transects are illustrated in Figure 8.

The transects, in order from north to south are described as to their salient points below (Figures 10 and 11).

Transect A, at Lake Pinjar south, at the junction between Spearwood Dunes and Bassendean Dunes, is located across the central western part of a large shallow basin. The sedimentary sequence in this part of the basin consists of a thin diatomite overlying a moderately thick diatomaceous muddy sand, with an apron of quartz sand derived from the uplands to the west deposited on, and pinching out over the diatomite deposits to the east.

Transect B, at Melaleuca Park, within the Bassendean Dunes, is located across a small, moderately symmetrical basin, with a simple fill of peat overlying a transitional layer of peaty sand. The upper surface of the peat has

Table 7

Sediment types of the three facies of wetland basins

Central facies	Basal facies	Marginal facies	Typical examples
calcilutite	muddy (calcilutaceous) sand	carbonate intraclast sand/gravel; organic matter enriched calcilutite; muddy (calcilutaceous) sand; spongolitic/phytolithic muddy (calcilutaceous) sand	Lake Manning Lake Coogee Wetland 163, Becher Point
diatomite; organic-matter-enriched diatomite	muddy (diatomaceous) sand	diatomite intraclast sand/gravel; organic matter enriched diatomite; muddy (diatomaceous) sand	Lake Mariginiup Lake Jandabup Gnangara Lake North Lake
peat	peaty sand	peat intraclast sand/gravel; peaty sand	Karrinyup Road Swamp Lake Mealup Beenyup Swamp

been cracked, brecciated (Fig. 8), and fire-sculptured (*cf.* Semeniuk & Semeniuk 2005).

Transect C, also at Melaleuca Park, within the Bassendean Dunes, is located across a small, moderately symmetrical basin, with a simple fill of peat overlying a transitional layer of peaty sand. In this wetland, following a history of fire, the peat has been reduced to a diatomite (essentially a residual ash) that blankets the floor of the wetland.

Transect D, at Ellenbrook, is located across a small basin within the Pinjarra Plain. It is filled with fluvially delivered kaolinitic muddy sand.

Transect E, at Lake Jandabup, within the Bassendean Dunes, is located across a large irregularly shaped basin floor, with asymmetry in thickness of sedimentary fill. Diatomite dominates the western part of the basin, and pinches out eastwards. The eastern part of the wetland is sand-floored, and its shore is comprised of a large beachridge system that has developed by wave and wind reworking of the sand exposed along the basin floor. Diatomite also occurs in the inter-beachridge swale east of the main basin.

Transect F, at Beenyup Swamp, within the Spearwood Dunes, is located across a large broadly symmetric basin filled generally with a simple sequence of peat formed asymmetrically from east to west, with simple relationship to the underlying and lateral sand. The surface lithologies of the deposit are fibrous peat, interlayered fibrous peat and local lenses of diatomaceous peat, and brecciated peat (Fig. 8). At depth, within the root-structured and fibrous peat, there are charcoal horizons (Fig. 8).

Transect G, at Little Carine Swamp, within the Spearwood Dunes, is located across a small slightly asymmetric basin filled with a complex sequence of a basal peat and an upper (shelly) calcilutite, with an inter-digitating relationship between the wetland fill and its margins. Peaty sand underlies the basal peat unit, and forms tongues that extend from the sandy margins of the wetland to a limited extent towards the basin centre.

Transect H, at Lake Gwelup, within the Spearwood Dunes, is located across a large asymmetric ancestral basin, with a highly irregular floor, filled with a complex sequence mainly of peat and calcilutite. There is an intrabasinal facies change with peat dominated sequences to the east in the shallow parts of the ancestral basin, and calcilutite dominated sequences to the east in the deeper parts of the ancestral basin. The margins of the wetland, under the influence of vegetation and its detritus, is dominated lithologically by organic matter enriched sediments. The upper layer of the calcilutite-filled eastern basin is organic matter enriched calcilutite (with scattered shell), that has sharp to gradational contact with underlying calcilutite (Fig. 8). The central basin sediments have a gradational facies relationship between the wetland fill and its margins, grading into organic matter enriched calcilutite, and then into peaty sand. Locally, in the lower part of the peat-dominated eastern part of the basin, there is lithological variation, with diatomaceous muddy sand forming the lowest unit in the sequence, underlying peaty sand (Fig. 8); this sequence is a facies variant outside the E-W transect illustrated in Figure 10).

Transect I, at Karrinyup Road Swamp, within the Spearwood Dunes, is located across a large asymmetric basin filled dominantly with peat. Within the peat sequence, fibrous, massive, root-structured, and laminated peat can be distinguished. There is a lens of thin diatomite (showing "seat earth") at depth, which pinches out to the east and to the west. Within the horizon of the diatomite, there is a small unit of diatomaceous peat. The lateral relationships of the main body of peat, along the edge of the basin, are gradational into sand, via peaty sand, or inter-digitating with sand tongues extending out into the wetland basin. The floor of the basin is generally peat directly overlying quartz sand with incipient development of thin peaty sand.

Transect J, at Kenwick Swamp within the Pinjarra Plain, shows basins filled with fluvially delivered interlayered and laminated mud, sand and muddy sand. A ferricrete sheet locally underlies the Holocene wetland sediments, and extends discontinuously under the Pleistocene sediments at the level of the water table.

Transects K, at Brixton Swamp within the Pinjarra Plain, is located across a small basin naturally excavated into Pleistocene sediments. The natural excavation has removed the surficial sand to expose underlying muddy sediments, which form the floor of the basin. The excavation has a veneer of kaolinitic mud.

Transect L at Lake Manning, in the Spearwood Dunes, is located across a large, deep, somewhat symmetrical basin, largely filled with grey to cream, laminated calcilutite, with lamination locally punctured by burrow structures (Fig. 8). In detail, the calcilutite sequence in the central basin also exhibits thin, laminated layers (1–2 cm thick) of organic matter enriched calcilutite and organic matter layers that extend across the basin. The margins of the basin, which appear to have been inhabited in the long term by peripheral vegetation, wherein the marginal facies has been generated, are underlain by organic matter enriched calcilutite, and locally peat; these organic matter rich sediments are consistently present in the stratigraphic profile as a marginal facies and not in the central facies. The base of the sequence is muddy sand (calcilutaceous muddy sand, or locally, diatomaceous muddy sand; Fig. 8) in the central basin or calcilutaceous muddy sand and peaty sand towards the basal margins of the basin.

Transect M, at Little Rush Lake, in the Spearwood Dunes, is located across a relatively small basin with an irregular floor. It is filled by peat. The eastern margin and the basal contact is peaty sand, gradational between peat and the underlying sand. The western margin has tongues of sand extending into and interlayered with the peat.

Transects N and O, across both un-named basins near Folly Pool, on the Pinjarra Plain, are located across small basins filled with fluvially derived sand and kaolinitic mud, respectively. The sand-filled basin appears to be an abandoned fluvial channel, now acting as a sediment trap reservoir.

Transect P, at Point Becher wetland 162 (C A Semeniuk 2006), within the Quindalup Dunes, is located across a small wetland showing a symmetrical basin floor shape, and gradual fill of the basin by infiltration of carbonate mud into the underlying sand (of the Safety
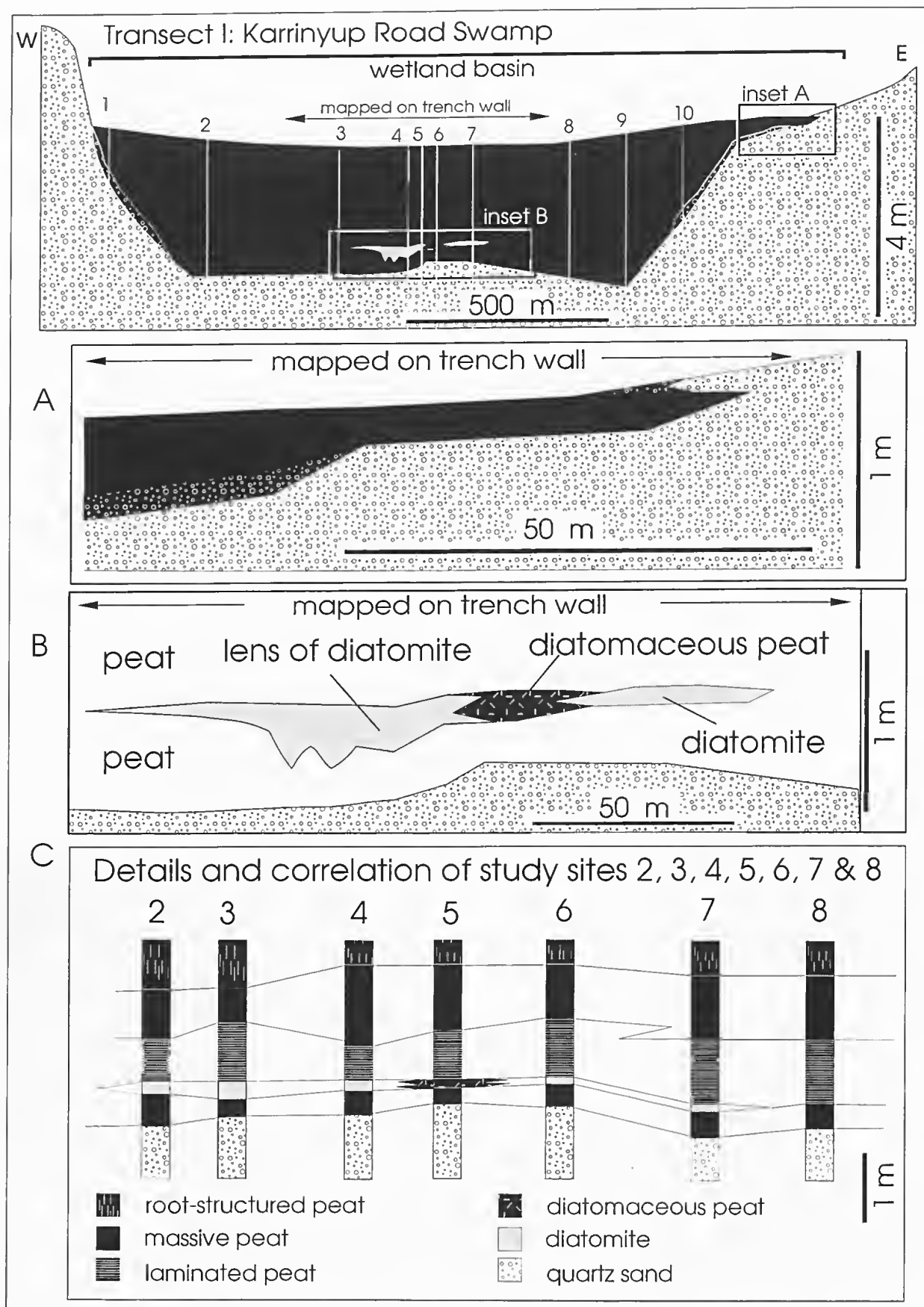
Figure 11. Transect I, Karrinyup Road Swamp, showing stratigraphy. Inset A: Detail of marginal stratigraphy and, on adjoining page, photographs A-D of cores from sites along the margin. Inset B: Diatomite interlayered with peat and, on adjoining page, photographs E–H of peat and contact of diatomite with peat (sharp lower contact, and root-structured upper contact, similar to "seat earth" where coal seams overlie clay or sand, *cf.*, Holmes 1965; Bates & Jackson 1987); lens cap in F is 50 mm diameter. Inset C: Stratigraphic correlation of sites 2-8.
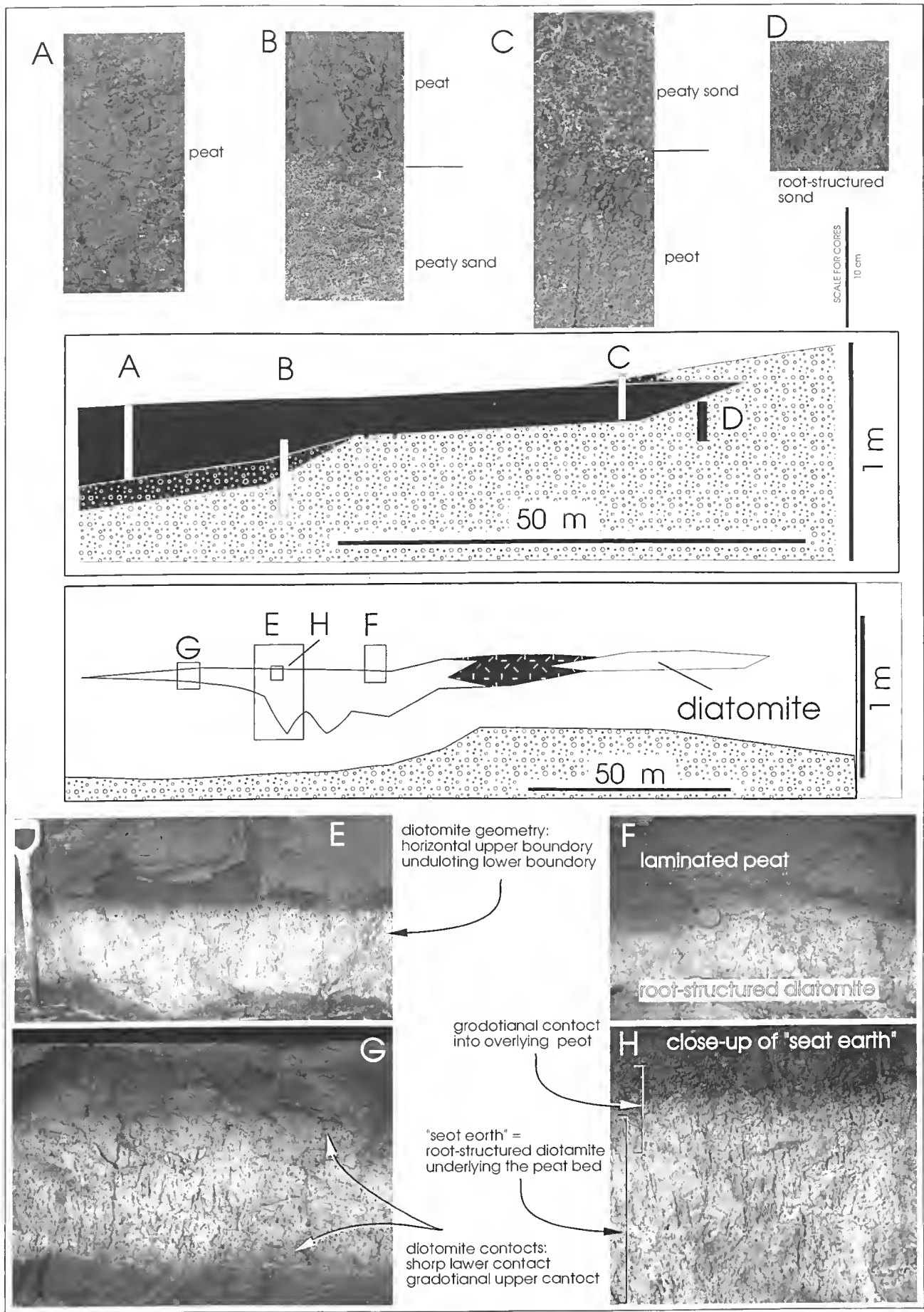
Figure 11 (cont.)

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Bay Sand) to form calcilutaceous muddy sand, by calcilutite, and then by peat. Over its history, due to hydrochemical and geochemical changes, the floor of the basin has subsided (C A Semeniuk 2006).

Transect Q, at Point Becher wetland 163 (C A Semeniuk 2006), within the Quindalup Dunes, is located across a small wetland showing a symmetrical basin floor shape, and gradual fill of the basin by infiltration of carbonate mud into the underlying sand (of the Safety Bay Sand) to form calcilutaceous muddy sand. The margins of the wetland show that there have been sand incursions into the wetland, resulting in tongues of sand extending over and burying the edge of earlier wetland deposits. The base of the wetland shows that it too had a complex history, with a two-staged development of initiation of wetland conditions. Over its history, due to hydrochemical and geochemical changes, the floor of the basin has subsided (C A Semeniuk 2006).

Transect R, at Point Becher wetland Wawa (C A Semeniuk 2006), within the Quindalup Dunes, is located across a small wetland also showing a symmetrical basin floor shape. It shows a gradual fill of the basin by infiltration of carbonate mud into the underlying sand (of the Safety Bay Sand) to form calcilutaceous muddy sand, followed by organic matter enriched calcilutite, and finally a capping of peat. The floor of the basin, due to hydrochemical and geochemical changes, has subsided (C A Semeniuk 2006).

Transect S, at Point Becher wetland sw-ii (C A Semeniuk 2006), within the Quindalup Dunes, is located across a small and young wetland showing a symmetrical basin floor shape, and gradual fill of the basin by infiltration of carbonate mud into the underlying sand (of the Safety Bay Sand) to form calcilutaceous muddy sand.

Transect T, at Lake Mealup, located across in a wetland occurring at the junction between Spearwood Dunes, Bassendean Dunes and Pinjarra Plain, illustrates a complex setting for a wetland basin. The basin floor is largely asymmetrical. To the east, it is underlain by muddy sediments of the Guildford Formation (that underlie the Pinjarra Plain); to the north and northeast, it is underlain by quartz sand (Bassendean Sand of the Bassendean Dunes), and to the west it is underlain by quartz sand and limestone of the Spearwood Dunes. As a result, the basin floor, i.e., the Pleistocene/Holocene unconformity, is underlain by muddy sand to the east, and quartz sand to the west. The basin has been filled in two stages: the lower part of the basin depression itself to the east consists of kaolinitic mud; peat, however, constitutes the main sedimentary fill in the basin, dominating the western part. The peat sequence consists of root-structured, bioturbated, fibrous peat to brecciated peat in the upper layers, and root-structured, bioturbated fibrous peat to laminated peat in lower layers (Fig. 8). Locally, at about a depth of 1 m, there is a thin lens of diatomaceous peat. The peat has a gradational (peaty sand) contact with any underlying sand, and a sharp contact with the kaolinitic mud. The upper eastern shore is marked by a shoe-string deposit of sand, which also is part of the wetland complex. This sand body is a beachridge accumulation that lies on muddy sand of the Guildford Formation, and is onlapped by the peat deposits of the central basin. The western shore, in a

gradient towards the high water mark, is underlain by peaty sand, organic matter enriched sand, and sand.

Transect U, at Willie Pool, in the Bassendean Dunes, is located across a small basin, with asymmetric ancestral shape. It is filled with peat (and some diatomaceous peat), that has gradational contact (peaty sand) laterally and basally with the underlying Bassendean Sand. The western accumulation of peat is thicker than the eastern part, and extends higher in the profile in relation to the high water level.

Transect V, at Crampton Swamp, in the Bassendean Dunes, is located across a small basin, with symmetric basin floor shape. It is filled with thin peat that has gradational contact (peaty sand) laterally and basally with the underlying Bassendean Sand.

Geographic distribution of stratigraphic types in wetlands

As with composition of surface sediments, the stratigraphy of the wetland fills varies according to geologic and geomorphic setting, climate, and host water chemistry. Hence, there is a pattern of stratigraphic sequences in an east-west transect, and from south to north on the Swan Coastal Plain. The east-to-west distribution can be related to consanguineous suites, and the south-north distribution is related to consanguineous suites and to climate. A summary of the east-west pattern of sedimentary fills in wetlands in relation to consanguineous setting in the central part of the Swan Coastal Plain is presented in Table 8.

Table 8

Dominant autochthonous sedimentary sequences in key consanguineous wetland suites, central Swan Coastal Plain.

Consanguineous wetland suite	Dominant stratigraphic sequence
Becher	calcilutite
Peelhurst	calcilutite, organic matter enriched calcilutite
Cooloongup	calcilutite
Yanchep	calcilutite, peat
Stakehill	calcilutite, peat
Coogee	calcilutite
Balcatta	peat, calcilutite
Bibra	diatomite
Pinjar	diatomite
Gnangara	diatomite, peat
Jandakot	peat, diatomite
Riverdale	peat, diatomaceous peat
Bennett Brook	peat, kaolinitic mud, muddy sand
Mungala	kaolinitic mud, muddy sand

Key processes in wetlands to develop sediments, structures, diagenetic products, and stratigraphic contacts and sequences

There is a range of processes that occurs within wetlands that generates distinctive sedimentary products in terms of sedimentary particles, sediment types, sedimentary structures, and diagenesis, and various stratigraphic contacts and sequences. While details of these processes and products, for use as a template to interpret Holocene wetland stratigraphy, will be the

subject of a later paper, a brief description of some of the key processes and products is provided here as they have a bearing on understanding the origin and significance of wetland sediments and stratal types described in this paper, as will be dealt with later in the Discussion and Conclusions. These processes often are location-specific, *i.e.*, they occur in definite environments in relation to the wetland centre or margins, or are associated with specific biotic zones. In addition to intrabasinal processes, there are regional factors, such as climate fluctuations and/or unidirectional climate changes during the Holocene, or groundwater chemistry changes that may play a part in influencing wetland stratigraphy and causing changes or alternations in lithology.

The key processes occurring within wetlands are: 1. biogenic sediment production; 2. infiltration; 3. bioturbation; 4. *in situ* vegetation accumulation; 5. organic matter contribution; 6. sponge spicule accumulation; 7. phytolith accumulation; 8. margin of wetland sedimentation and shoreward transport; 9. deep water accumulation; 10. desiccation; 11. pyrogenesis; 12. winnowing; 13. delivery of fluvial mud and sand; and 14. alternating hydrochemistry. They are described in Table 9 in relation to their products, and location within a wetland.

The issue of hydrochemical changes is discussed in more detail here because it is a significant one that relates to interpreting sedimentary sequences. It is important to recognise that lithologic changes and lithologic alternations may be due to: 1. regional factors such as a changing climate (*e.g.*, a general change in climate from relatively arid to relatively more humid, as driven perhaps by Earth-axis precession; see Semeniuk 1995), and manifest, for example, by a change in gross stratigraphy from calcilutite to peat, or a change in stratigraphy from calcilutite to organic matter enriched calcilutite, 2. a fluctuating climate (*e.g.*, a 250-year cycle; see Semeniuk 1995), resulting in finely interlayered calcilutite and peat, or finely interlayered calcilutite and organic matter enriched calcilutite, or 3. hydrochemical changes in the wetland basin (see C A Semeniuk 2006). In the Becher area, C A Semeniuk (2006) determined that many of the vegetation changes within a wetland basin were due to intrabasinal hydrochemical evolution as related to vegetation influencing salinity of the shallow groundwater, which, in turn, resulted in changes in vegetation. In that context, in the Becher area, a range of different basins with variable hydrochemical history showed a varying vegetation history that reflected intrabasin factors and not regional climatic factors – such vegetation changes can translate to a varying lithology in their contribution to sediment (to form peat), and/or modification of sediment to form organic matter enriched calcilutite. As such, it is important to be able to distinguish lithological changes generated by hydrochemical evolution or fluctuations, from those induced from unidirectional climate change, or climate fluctuations.

Synthesis, discussion and conclusions

This synthesis and discussion focuses on eight features of wetland sedimentology, and stratigraphy, and their implications for understanding hydrology, ecology and management: 1. the variability of sediment thickness in a wetland basin; 2. the nature of the basal facies; 3. the range of primary sediment types across the Swan Coastal Plain related to setting; 4. the lateral facies variation in stratigraphy within a wetland basin; 5. homogenous *versus* heterogeneous stratigraphic sequences; 6. stratigraphy as a measure of hydrochemical and biotic stability, and hence palaeo-environmental history; 7. the asymmetry of stratigraphy; 8. the significance of stratigraphy to hydrology; and 9. the significance of stratigraphy to plant ecology.

The variability of thickness of the various sediment types and total thickness of the basin sediment fill is related to the factors of availability of a given sediment type, the depth of original basin floors with respect to the final late Holocene regional water table, and sedimentation rates. For instance, low rates of influx of clay within a clay-poor setting would result in thin clay beds accumulating in a basin. But given adequate rates of sedimentation, the thickness of basin fill will depend on the depth of an original wetland basin floor at the time of inundation, when, with post-glacial rising sea levels, the water table rose to intersect the palaeo-land surface generally some 10,000–8,000 years BP. Local topographic depressions that were deep enough to be inundated early by a rising water table (sympathetically rising with sea level at the ending of the last ice age some 20,000 years ago) would have commenced sedimentation earlier, and would have developed the thickest sequences. Sediments would continue to fill a basin until the floor was built up to the highest water of the current regional water table level. Thereafter, wetland sedimentation processes largely would have ceased. Most of the wetlands basins encountered in this study had relatively shallow deposits of sediments, indicating that the floor of the original depressions (that were to become the floor of the wetland basin) were located more or less within the position of the present regional groundwater level. Some of the large lakes and wetlands, such as North Lake, Lake Manning, and Karrinyup Swamp, have several metres of sedimentary fill, indicating that they were relatively deep depressions at the time of the early Holocene, and were inundated early with the rising regional water tables at the end of the Pleistocene. On the other hand, other large lakes and wetlands such as Lake Mariginiup, Lake Jandabup, and Lake Pinjar, have relatively thin sedimentary fills, indicating that their ancestral floors were located near the position of the present regional water table. However, full exploration of this matter is beyond the scope of this paper, and will be investigated further, in combination with radiometric dating of wetland sequences, in a later paper (Semeniuk & Semeniuk, 2006, unpublished manuscript).

In Swan Coastal Plain wetland basins that are filled with fine grained sediment (either biogenic sediment or terrigenous sediment), the base of the sedimentary fill generally is a muddy sand basal sheet. This muddy sand sheet effectively signals the commencement of wetland sedimentation. As described by Semeniuk & Semeniuk (2004), processes of vadose infiltration and bioturbation combine to deliver fine grained wetland sediment into any underlying basement sand (the original ancestral floor of the wetland basin). The thickness of the basal muddy sand sheet varies, and would have depended on

Table 9

Processes, description and products, and location within wetlands

Process	Description and products	Location within wetland
biogenic sediment production	production of biogenic material by macrophytes, filamentous and unicellular algae, diatoms, and invertebrate fauna leading to the development of peat, diatomite, and calcilutite, and shell beds	depending on depth of water, and frequency of inundation, these biota and their products may be basin wide, or restricted to the margins of wetlands
infiltration	fine grained sediment infiltrating, by vadose processes, into underlying basement sand	along the base in the early stages of basin filling, and along the margins during later stages
bioturbation	fine grained sediment bioturbated by vegetation and fauna into underlying basement sand, and mixing and perturbation of any interlayered and laminated sediment; in modern environments, depending on the biota, bioturbation is most intense in the upper 10–20 cm of the sediment, but can be effective to 30–50 cm	basin-wide, but most common along the margins
in situ vegetation accumulation	accumulation of macrophyte plant material and its detritus where it is growing, resulting in the formation of fibrous to massive peat beds, or (in conjunction with degradation and bioturbation) organic matter enriched sediments	basin-wide in shallow water wetlands; restricted to margins in deeper water wetlands or where there is consistent peripheral vegetation
organic matter contribution	accumulation of macrophyte plant material and its detritus along margin, or transported into deeper water, to form organic matter enriched sediment, or deeper water peats	basin wide, or restricted to margins in deeper water wetlands or where there is consistent peripheral vegetation
sponge spicule accumulation	accumulation of freshwater sponge spicules after the death of the sponges, or after combustion of the supporting vegetation into sediments forming spongolitic peat and spongolitic diatomite	if sponges are restricted to peripheral vegetation, spicule accumulation is largely circumferential to the basin; in shallow water wetlands wholly covered by vegetation, spicule occurrence is basin-wide
phytolith accumulation	sedge assemblages upon their death and decay, or combustion in a fire, yield phytoliths and contribute particles to the sediments	if sedges are peripheral to a wetland, accumulation is largely circumferential to the basin; in shallow wetlands wholly covered by vegetation, phytolith contribution is basin-wide
margin of wetland sedimentation and shoreward transport	various processes result in preferential deposition of sediments in margin zones; these include transport by wave and currents of fine grained sediment via suspension to the wetland margin and its accumulation there (usually amongst peripheral vegetation); and wave transport of sand by traction to shorewards	margin of wetland
deep water accumulation	accumulation of fine grained matter, such as carbonate mud, plant detritus, diatoms, unicellular algae, carried in suspension and settling in deep water	deep water parts of wetland
desiccation	drying out and cracking of sediments to form gravel and sand intraclasts of peat, diatomite and calcilutite	largely confined to margins, though for shallow water wetlands; this can be basin-wide (*e.g.,* peat breccia can form a surface basin-wide horizon)
pyrogenesis	combustion by fire consumes peats, and can generate organic-matter-free lithologies such as diatomite; by cracking sediments generates intraclasts; forms sand lenses and ash deposits (Semeniuk & Semeniuk 2005)	largely confined to margins, though for shallow water wetlands; this can be basin-wide (*e.g.,* peat breccia generated by fire can form a surface basin-wide horizon)
winnowing	wave action and currents winnow sandy and gravelly muddy sediments to leave coarse lags such as shell beds, and intraclast deposits	largely confined to margins, though for shallow water wetlands; this can be basin-wide
delivery of fluvial mud and sand	floods carry kaolinitic mud in suspension and quartz sand by traction to basins on the Pinjarra Plain, progressively filling them with these sediments	fluvial delivery of terrigenous sediments fills the interior of the wetland basins
alternating hydrochemistry (see below)	an alternation of hydrochemistry driven by alternating vegetation succession changes the composition of the flora and fauna, leading to an alternation of processes (described above) and to alternation of lithology	this process can be restricted to the wetland margins; depending on the depth of a wetland, it can also be basin-wide

the organisms involved in the bioturbation. Shallow rooted plants effect bioturbation to depths of 10–20 cm; trees effect bioturbation to depths more or less of 40 cm; foraging mammals effect bioturbation to depths of 10–15 cm; burrowing crustaceans dig burrows as deep as 50 cm; and insects and other invertebrates burrow to depths of 5–30 cm. The effect is that fine grained sediment, delivered by fluvial processes, or generated biogenically in the basin, is bioturbated into the underlying basement sand to form a muddy sand sheet (viz., kaolinitic muddy sand, peaty sand, diatomaceous muddy sand, and calcilutaceous muddy sand).

The range of primary sediment types across the Swan Coastal Plain appears related to geologic/geomorphic setting and its attendant hydrochemistry. At one extreme, fluvially dominated systems of the Pinjarra Plain are dominated by kaolinitic clay and fluvial sand as wetland basin fills, and there is an absence of such terrigenous sediments in the dune-dominated landscapes of the Quindalup Dunes and Spearwood Dunes. Similarly there is an absence of such terrigenous sediments in the dune-dominated landscapes of the Bassendean Dunes, though there is terrigenous clay in the fluvially over-printed landscape of the Bassendean Dunes in wetland settings such as the Bennett Brook Suite (C A Semeniuk 1988). Carbonate sediments dominate wetlands located in carbonate terrains of the Quindalup Dunes and Spearwood Dunes, implicating the geochemical (carbonate) foundations of the wetlands as the hydrochemical source that drives these systems. Where macrophytic vegetation and diatom populations have been sufficiently productive, wetlands set in carbonate terrains may develop peat and diatomaceous peat, but often such wetlands have a stratigraphy that indicates alternating calcilutite-dominated and peat-dominated sedimentation. Diatomite and peat dominate the wetlands located in the quartz sand rich terrain of the Bassendean Dunes, and carbonate mud production is not (and was not) a feature of these carbonate-poor terrains. Where peat production by macrophytes was relatively low, diatomites dominate, and where peat was formed, peat and diatomaceous peat were developed.

While there is a change in sediment composition across the Swan Coastal Plain in relation to geology/geomorphology and hydrochemistry, there are also lateral facies variations in stratigraphy within wetland basins. In the first instance, the sediment facies variation can be related to the physico-chemical and biological gradients that occur from the central basin to the margin of the basin. That is, permanently inundated, or otherwise deeper parts of the wetland basin, with a more consistent aquatic or water-saturated environment, will grade to the margin environments where physico-chemical processes, such as wave action, desiccation, chemical precipitation, amongst others, as described earlier, that are specific to wetland margins, combine to create distinctive sedimentary products. Wetland margins are also zones where there may be biota assemblages contributing organic matter to the sediment, or contributing sponges spicules and phytoliths to the sediment, and where wetland sediment fill interfaces with the basement materials. A summary of the idealised lithological nature and stratigraphy of wetland basins in terms of basal facies, marginal facies, and central facies

for diatom-dominated, calcilutite-dominated, and peat dominated basins, is shown in Figure 12.

However, in addition, there are also facies changes in wetland basins *within* the central facies. For instance, at Lake Gwelup, for the equivalent thickness of several metres of its sedimentary fill, the basin is dominated by peat in its eastern part, and dominated by peat overlying calcilutite in its western part. Karrinyup Road Swamp shows a particularly interesting lithologic change in the central facies: a lens of diatomite, some 50 cm thick, passes laterally into diatomaceous peat and then to peat over some tens of metres. On the other hand, a large number of large wetland basins show little variation in lithology within the central basin, e.g., the calcilutite of Lake Manning, the diatomite of Lake Pinjar, and the peats of Beenyup Swamp, Willie Pool and Lake Mealup. Lateral lithologic homogeneity is particularly the case for small basins. For example, apart from the marginal and basal facies, the central basin lithology of wetlands in the Becher Suite is dominated by calcilutite, and small basins in the Jandakot Suite and Riverdale Suite in the Bassendean Dunes are dominated by peat and diatomite, and peat, respectively.

One of the most interesting aspects of the vertical sedimentary fill of the wetlands is whether their central facies is stratigraphically homogenous or heterogeneous. The wetlands of the Becher Suite (calcilutite-filled), those in the Coogee Suite (calcilutite-filled), certain basins in the Yanchep Suite (e.g., Waluburnup Swamp which is peat-filled), and many of the wetlands of the Jandakot Suite, Riverdale Suite, and Gnangara Suite (peat or diatomite filled) display relatively homogeneous stratigraphy vertically. In contrast, wetlands either located in the Spearwood Dunes or at the interface between the Spearwood and Bassendean Dunes may exhibit vertical stratigraphic heterogeneity: for example, Lake Joondalup, Little Carine Swamp, Balcatta Swamp, Leda Swamp, The Spectacles, and Bollard Bullrush Swamp.

In a geohistorical sense, over the period of the Holocene, the vertical homogeneity or heterogeneity of wetland stratigraphy is an important issue. It can be used as a measure of hydrochemical stability and hence biotic stability. For example, if it is accepted that hydrochemical and hydrological patterns regulate biotic response, then the consistent occurrence of calcilutite (generated by breakdown of charophytes; cf. Semeniuk & Semeniuk 2004) over, say, 5000 years of stratigraphic record, signals an environment relatively hydrochemically and hydrologically stable. Wetlands wholly and consistently filled with peat derived from, say, *Baumea articulata*, similarly signal relative hydrologic and hydrochemical stability over the period of peat accumulation. On the other hand, wetlands that are filled with sequences that change from peat to diatomite to calcilutite, or that alternate between lithologies, signal changes in the hydrochemical environment within the wetland. This is a particularly important matter to note when at the same time, over the same period of the Holocene, wetlands elsewhere are not exhibiting such dynamics, and thus it provides an insight from a stratigraphic perspective of the long-term (natural) comparative hydrologic, hydrochemical and biological stability of individual wetlands. Information on these stratigraphic signatures
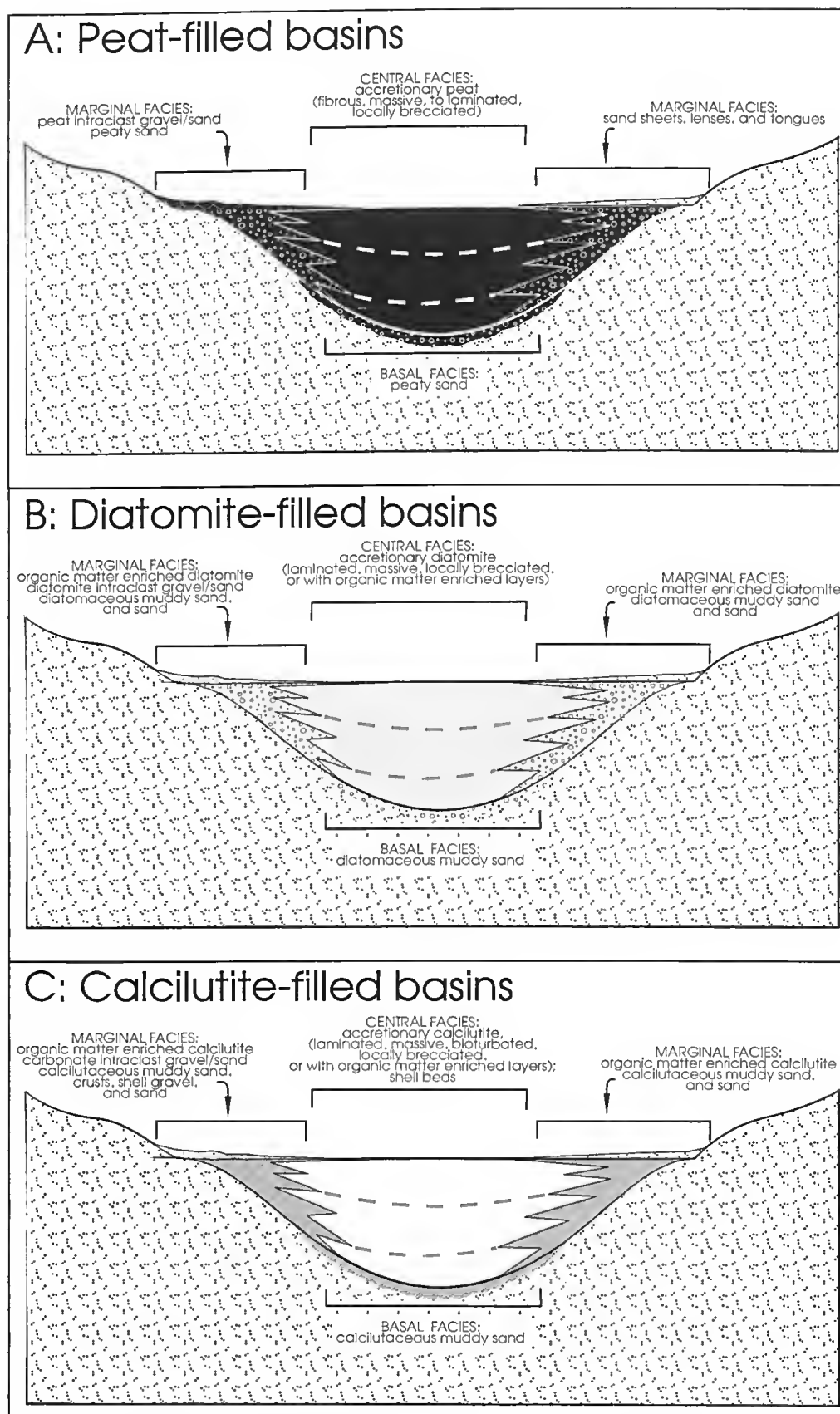
Figure 12. Summary annotated diagram showing idealised lithological nature of the basal facies, central basin facies, and marginal facies for peat-filled, diatomite-filled, and calcilutite-filled basins, and their stratigraphic relationships. Because of the complexity and variety of sediments that are formed in the marginal facies, the left hand side of the marginal facies of each of the basin sedimentary fills highlights only those lithologies formed specific to the inner marginal facies (with sources of sediments mainly from the central basin), while the right hand side of the marginal facies highlights sediments produced by as a result of incursions of sand into the basin (with sediment reworked or shed mainly from basin margins, *i.e.*, extrabasinal), without implication that there is consistently such asymmetry within the basins. The emphasis in this diagram is on intrabasinally derived biogenic sediments systems.

of long-term and medium-term wetland ecosystem stability has important implications for understanding wetland management.

The alternations in lithology within wetland basins, and how it is interpreted have palaeo-environmental implications. It is necessary to separate those alternations due to climate changes, from those induced by alternating hydrochemical changes or unidirectional hydrochemical evolution of wetlands, from those induced by ecological processes (linked to hydrochemical changes). Sediments within wetland basins are autochthonous (*i.e.*, formed intrabasinally), and therefore provide a more reliable indicator to separate hydrochemical and ecological changes from climatic changes. To date, climate changes have been inferred from mainly extrabasinally derived pollen rain. Future research could be directed to the study of palaeo-hydrochemistry, and hydrochemical history, as reflected in wetland sediment through their fossil biota.

Stratigraphy has another important role to play in wetland management, *viz.*, in the arena of wetland hydrology, and plant ecology. For the Swan Coastal Plain, Townley *et al.* (1993) provide a series of hydrological models of groundwater flow through wetlands (specifically lakes), for unconfined aquifers, but deal with large-scale hydrological processes, identifying perched lakes, groundwater recharge lakes, groundwater discharge lakes, and groundwater throughflow lakes. One of the important factors in the treatment of groundwater interactions with wetlands is the local effect of wetland sediments on groundwater flow (*i.e.*, wetland sediment thickness, their geometry, transmissivity, and nature of contact with the surrounding terrain), as this will perturbate groundwater patterns at the local scale, the scale at which groundwater enters a wetland and the scale at which peripheral vegetation responds to hydrological processes. As a consequence, the small-scale stratigraphic relationship along wetland margins becomes important, as this will influence small-scale hydrologic processes, and depending on lithology, hydrochemical products along the wetland margin. C A Semeniuk (2006) emphasised this factor in the study of hydrology around the individual wetland basins in the Becher Suite. The Becher wetlands are a rain-fed recharge system that translates to a regional throughflow system. Depending on the thickness and complexity of the sedimentary fill of these wetland basins, there are perturbations at the local scale to the regional throughflow pattern, culminating in variable degrees of local diversion of flow in the various wetlands, and in places, upwelling (C A Semeniuk 2006). In addition, in the Becher wetlands, how water is delivered to a wetland from up-slope sources often depends on the stratigraphic nature of the wetland margins, *i.e.*, whether there are sheets and tongues of sand that penetrate into the wetland sediment sequence.

In this context, from a stratigraphic perspective, we suggest that the small-scale stratigraphic relationships along the base and margins of the wetlands, and the nature of stratigraphic layering (resulting in variable transmissivity) should be significant factors to consider in determining how regional groundwater enters into, percolates through, and discharges from a wetland basin. This will be a small scale hydrological feature critical to

management of wetland hydrology if wetlands are to be environmentally sustained or managed rigorously.

At medium and large scales, stratigraphy, in conjunction with hydrology as outlined above, also has a role to play in plant ecology. The variety of stratigraphic contacts, in terms of geometry and lithology, and their associated hydrological and hydrochemical processes will influence plant associations along the margins of wetlands. To date, there has been a tendency only to examine the surface material (what authors generally term the "soils"), but we suggest that stratigraphy is a factor that needs to be addressed to understand the distribution and maintenance of plant associations, particularly at the finer scales, in any phytoecological study of wetlands.

Also, at the large scale, asymmetry in stratigraphy needs to be addressed in holistic environmental studies. This asymmetry may be due to: variable biogenic production rates across a wetland basin; variable transport mechanisms and sink sites across a basin; an irregular ancestral basin shape; variable hydrological factors in response to regional groundwater table gradients; or a variable cross-basin fire history. Asymmetry in stratigraphy can lead to asymmetry in hydrological function, in geochemistry, and hydrochemistry, and hence in biota. The result stratigraphically will be expressed as variation in lithology across a basin, and/or variation in sediment thickness across the basin, and variation to the extent that sediments occur above the mean high water datum. This large-scale pattern of stratigraphic asymmetry underlying wetlands has not been adequately addressed in the analyses of the phytoecology or macroinvertebrate ecology of wetlands, and we suggest it is an underlying determinative factor in the larger scale ecological functioning of wetlands, and hence in the proper management of wetlands. Also, any asymmetric stratigraphic pattern may have an interactive feedback relationship with vegetation. That is, the asymmetry in stratigraphy across a basin may alter the hydrologic functioning and processes across a wetland to the extent that vegetation and other biota respond in terms of the types of assemblages that may inhabit the wetland margins, or in their rates of primary or secondary production, which in turn results in a contrast in sediment accumulation rates, hence further amplifying the asymmetry in sediment thickness, or amplifying the contrast in facies.

From the results of this paper, we emphasise that to fully investigate wetland stratigraphy, with all that is recorded sedimentologically, biologically, and diagenetically, and to fully interpret the stratigraphic sequence lithologically, there is a need, firstly, to place sedimentary sequences in a geologic, geomorphic and hydrochemical context, and secondly, to construct across-basin stratigraphic relationships for a given wetland basin. Such an approach, as mentioned in the Introduction, places palaeobiological sequences and a single-core lithological sequence for large wetland basins in a context. It provides a more comprehensive database for reconstruction of wetland palaeo-sedimentology and history, provides a framework for hydrologic processes and functions, and provides a framework for determining and understanding ecological processes,

ecology patterning (*e.g.*, zonation), and biodiversity. We suggest also that the stratigraphic approach adopted in this paper should form the foundation for unravelling the sedimentological, hydrologic, hydrochemical, climatic and biologic history of the wetlands across the Swan Coastal Plain, and for understanding current wetland hydrology and wetland vegetation ecology.

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